FOOD RESOURCE UTILISATION BY *TENAGOMYSIS CHILTONI* (CRUSTACEA, MYSIDACEA)

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ABSTRACT

The interrelationships existing between some different parameters which may have influenced the diet of *Tenagomysis chiltoni* (Crustacea, Mysidacea) were investigated in Lake Ellesmere, South Canterbury, New Zealand (43°48'S, 172°22'E). The mysid was found to be omnivorous and ingested foods having both aquatic and terrestrial origins. The stomach contents of 1113 mysids were examined. The diet was mainly composed of macrophyte detritus, filamentous algae, diatoms, calanoid and harpacticoid copepods, chironomids, amphipods and ostracods.

Seasonal variations in the length-frequency structure of *T. chiltoni* populations were observed. These variations were due to the emergence and development of successive broods. An associated variation in the male:female ratios was found, and may be due to males dying out before females belonging to the same cohort.

The most important intrinsic factor exerting an influence on the diet of an individual was the length of a mysid which was partly dependent on the sex of an individual. Hunger did not affect the nature of the foods ingested.

Changes in the length-frequency structure of the population were observed which influenced the quality and quantity of the diet of *T. chiltoni*. Some environmental parameters also influenced the quantity ingested. The nature of the water column and, to a lesser extent, benthic food resources, regulated the selection of diet by the mysid which was controlled by physical considerations. Seasonal cyclical variations in the availability of some food resources caused changes in the diet of *T. chiltoni*.

The observed diet of *T. chiltoni* is a product of the complex interaction of intrinsic and extrinsic factors and varies in space and time.

CHAPTER 1

GENERAL INTRODUCTION

Tenagomysis chiltoni was originally described by Tattersall (1923) and subsequently redescribed by Hodge (1964); no significant studies on the species have been published since, although it has occasionally been recorded in general ecological studies.

The distribution of *Tenagomysis chiltoni* throughout New Zealand is inadequately known, but is more extensive than was noted by Mauchline and Murano (1977). It is present in many coastal lagoons, rivers and at least a few freshwater lakes in the North Island (Hodge, 1964; Jolly and Brown, 1975; P. Kirk, pers. comm.). In the South Island *T. chiltoni* is found in Lakes Ellesmere and Forsyth, Coopers Lagoon, and their inflows. *Tenagomysis chiltoni* also occurs together with *Tenagomysis novaezelandiae* in the Avon-Heathcote Estuary (Greenwood and Jones, pers. comm.). Further to the south *Tenagomysis chiltoni* appears to have been replaced by *Tenagomysis novaezelandiae* in some coastal lagoons.

Tenagomysis chiltoni Tattersall is an important component of the fauna of littoral habitats in Lake Ellesmere, Mid-Canterbury (43°48'S, 172°22'E; N.Z.M.S. 1, S93/3, 770240, and adjacent maps). This lake is the fourth largest in New Zealand (data from Irwin, 1975) and the largest in Canterbury (Stout, 1969), having a surface area of 15,790 - 20,250 ha, depending on the level of the lake water (Griffiths, 1975), and an average depth of 2.1 m when the lake level is at Mean Sea Level (m.s.l.) (Hughes, McColl and Rawlence, 1974). The lake contains brackish water with a mean salinity of 20-30% that of sea water (Stout, 1969) dependent on freshwater inflow from the catchment area, saltwater influx from the sea and evaporation from the lake (Gorman, 1960). To protect bordering farmlands from the effects of saline impregnation the lake level is artificially regulated by cutting an outlet channel through the Kaitourete Spit to the sea when the lake's surface is about 1 m above m.s.l. The North Canterbury Catchment Board's records suggest variation in lake surface level between 0.3 and 1.58 m above m.s.l. between May, 1965 and August, 1981. The average depth when the lake surface is at m.s.l. is therefore not representative of normal conditions within the lake. The opening of the lake permits saline water to enter the lake, creating higher salinities closer to the

opening near Taumutu, with progressively decreasing salinities towards sites of freshwater influx. The maximum salinity recorded for the lake is 56% sea water (Stout, 1969), which is approached by salinities recorded in this study. The shallow nature of the lake causes high waves even in modest winds. The resultant wave-induced currents suspend large sediment loads, contributing greatly to the generally high turbidity of the lake water.

T. chiltoni was reported to occur, together with *Tenagomysis novaezelandiae*, as an important component of the fauna of Lake Ellesmere (Percival, 1955). *Tenagomysis novaezelandiae* was subsequently recorded in Lake Ellesmere by Griffiths (1975, 1976) who incorrectly identified *T. chiltoni* as *T. novaezelandiae*, a statement based on a re-examination of Griffith's specimens. At the time of the present study only *Tenagomysis chiltoni* was found in the littoral zones of Lake Ellesmere and the inflowing rivers sampled. The continued existence of *T. novaezelandiae* within the Lake Ellesmere system is therefore in doubt. In view of the alternative management strategies for the lake under review at present, a knowledge of the biology of *Tenagomysis chiltoni* within Lake Ellesmere may be required to prevent the disappearance of this valuable species.

In Lake Ellesmere *Tenagomysis chiltoni* grows to a maximum observed length of 19.5 mm, adult females being consistently larger than adult males. The species is therefore large compared with most species of this and other genera within the Order Mysidacea (Mauchline and Murano, 1977; Mauchline, 1980).

Tenagomysis chiltoni forms part of the diets of many of the smaller fish examined during this study, and also of *Anguilla australis schmidtii* (Ryan, 1978) which supports an export-orientated fishery worth $0.75 m Freight On Board annually; revenue accrued from commercial fisheries based upon Lake Ellesmere is estimated at $1 m (F.O.B.) (P. Todd, pers. comm.). In addition, the lake's fauna provides a valuable recreational resource for the benefit of angler, observer, photographer and shooter alike. The ecology of invertebrates within the lake is therefore of interest from economic, social and ecological viewpoints. *Tenagomysis chiltoni* is of especial interest due to its numerical abundance and value as a food organism, which suggest that *T. chiltoni* may be preferentially selected for by predators (Berman and Richman, 1974), and exert a disproportionate influence in relation to its abundance on the animal and plant associations within the lake (Brinkhurst, 1974).

Prior to the start of this project no work had been done on any aspect of the population dynamics of *Tenagomysis chiltoni*, or been published on the population dynamics of any member of the genus *Tenagomysis*. The only reference to the feeding of *Tenagomysis chiltoni* concludes that it feeds on a diet partly composed of plant detritus (Chapman and Lewis, 1976). Marples (1962) refers to digestive tracts of *Tenagomysis novaezelandiae* containing unidentified insect fragments; as the author fails to acknowledge the existence of *T. chiltoni* in freshwater habitats of New Zealand the species identification is dubious.

The feeding ecology of the Order Mysidacea has received remarkably little detailed examination in view of the abundance of mysids in many ecosystems. Only one species of mysid, *Neomysis mercedis*, has been systematically studied for ontogenetic and seasonal changes in diet (Mauchline, 1980) in studies by Edmondson and Murtaugh (1980), Kost and Knight (1975) and Siegfried and Kopache (1980). Quantitative information on the availability of different foods has normally been sparse or absent, even though the potential food source forms a basis on which the feeding habits of different species can be compared (Berg, 1979). As the nature of the food resource may affect the choice of optimal diet (Emlen, 1966; Estabrook and Dunham, 1976; Pulliam, 1974; Pyke, Pulliam and Charnov, 1977) or selection of food by an organism (Kajak, Spodniewska and Wisniewski, 1977; Menge, 1972; Siegfried and Kopache, 1980), the examination of food availability is also crucial to understanding the ingestion observed and the extrapolation of results to the same species occurring in other regions. Mysids have physiological or behavioural responses to salinity differences (e.g., Simmons and Knight, 1975), light intensity (e.g., Beeton, 1959, 1960; Smith, 1970), temperature (e.g., Hakala, 1978) and wave action (e.g., Boroditch and Havlena, 1973), amongst other factors. As possible sources of disturbance capable of producing adaptive modification of the organism's movements, and hence its access to food resources, these factors also have to be considered. As so many factors have the potential to modify a mysid's ingestion, a comprehensive approach was required in this investigation which covers the ingestion by the organism, the availability of foods, population changes of *Tenagomysis chiltoni* and changes in environmental variables.

The research programme was therefore designed to quantify those factors most likely to induce modification of ingestion where this approach did not cause an undue amount of labour in proportion to the

probable degree of influence exerted by the modifying factor. The study relates only to the daylight feeding of *Tenagomysis chiltoni*; practical limitations prevented the investigation of diurnal changes in feeding, which are probably present in some species and not in others (Mauchline, 1980), and may be dependent on environment.

The objectives of the study were to investigate the composition of the diet of *T. chiltoni* (using volumetric transformations of numerical data on food organisms) and to relate food availability, collection site, collection time, mysid length, mysid sex and level of satiation, and to study the influence of selected physical parameters of the environment upon ingestion. As a subsidiary consideration, an investigation of the population dynamics and densities was conducted during the calendar year in which the main sampling programme was undertaken; this allowed an assessment of the relation of the influence of any individual's feeding to that of the whole population present at a given site and time, and over the whole study period.

CHAPTER 2

METHODS

2.1 INTRODUCTION

Samples were collected from a series of four sampling stations around Timberyard Point, Lake Ellesmere (43°48'S, 172°22'E; N.Z.M.S. 1, S93/3, 770240. The four sampling sites were selected because they represented different littoral habitats along a salinity gradient, created by the inflow of Harts Creek, along the northern shore of Timberyard Point (Fig. 1). It was hoped that the diverse habitats investigated would produce attendant differences in the food resources available at each site, with the outermost two sites typifying littoral habitats in the lake generally. The sites were designated M, 1, 2 and 3 in sequence from the marsh surrounding the mouth of Harts Creek eastwards along the shoreline of Timberyard Point to the final station 0.7 km south of the point. At each station the mysid population was sampled together with the available food resources, and certain environmental parameters determined.

Collections were made at an interval of one month, or as soon thereafter as climatic and logistic limitations permitted. Sampling commenced at approximately 1030 hours at site 3, followed by site M, then sequentially through site 1 to site 2 where sampling was completed around 1600 hours. The results of the investigation are therefore predominantly representative of ingestion by *T. chiltoni* during daylight hours.

2.2 FIELD SAMPLING PROCEDURES

2.2.1 General

On arrival at each site a systematic sampling routine was pursued as accurately as environmental conditions, in particular the lake level, allowed. Deviations in routine were minimal. A full set of samples was collected from each site regardless of whether mysids were present or absent at that time. The sampling procedure took approximately 45 minutes to complete at each station. Collections comprised small and large water column food resource samples, small and large benthic food

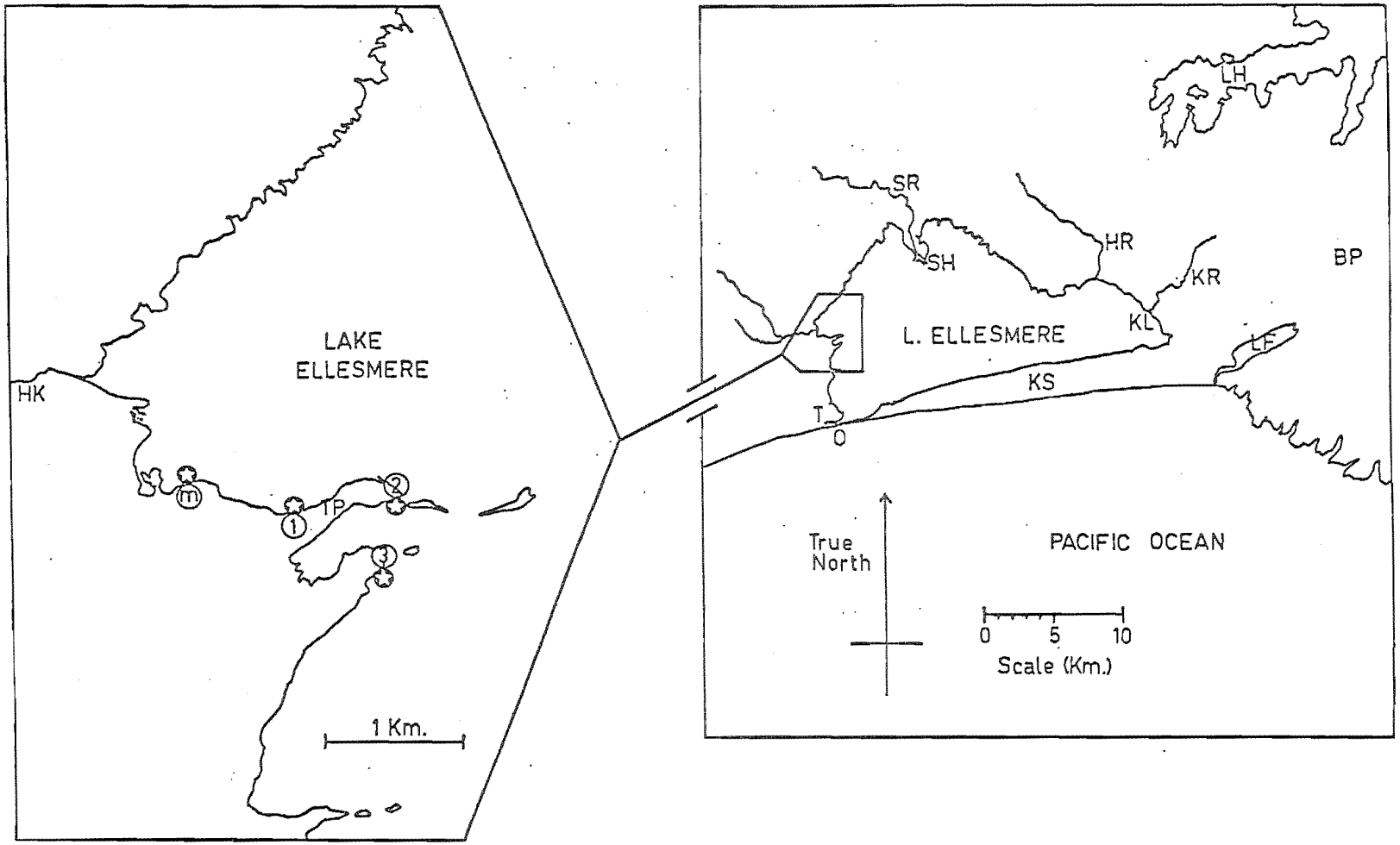

Fig. 1 Map of Lake Ellesmere and surrounding regions with an inset showing the location of sampling sites. The sampling sites M to 3 are marked with stars on the inset map. BP = Banks Peninsula, HK = Harts Creek, HR = Halswell River, KL = Kaituna Lagoon, KS = Kaitourete Spit, LF = Lake Forsyth , LH = Lyttelton Harbour, O = lake opening, SH = Selwyn Huts, SR = Selwyn River, T = Taumutu, TP = Timberyard Point.

resource samples, mysid samples and a water sample for the determination of dissolved oxygen and salinity. Each site had previously been marked with four bamboo stakes, 10 m apart, marking the ends of three 10 m sampling transects running obliquely down the littoral zone.

2.2.2 Small Water Column Food Resources

The small water column food resources sample was collected first to avoid contamination of the sample with material stirred up from the sediment and sediment water interface. The sample was taken 5 cm above the substrate by opening a 20 ml air-filled vial at this level and closing it at the same level when full of water. As only 20 ml of water was collected using this method, mixing of the water column by outrushing air was minimal. The method used was favoured over the use of a hypodermic syringe as the possibility of inflow aperture blockage was greatly reduced. Formaldehyde was added to make up a concentration of 4% immediately after collection.

2.2.3 Mysid Population

Samples of *T. chiltoni* were collected next. At the start of the programme the minimum size of a post-larval mysid of this species was not known. Therefore, as all the stages of *T. chiltoni* present at each station were required for the envisaged study, it was decided to use a hand net of 0.5 m diameter aperture and a mesh of 250 µm pore size to ensure that the smallest stages were collected (a mesh size of 500 µm is now considered optimal for population studies). Bowers and Grossnickle (1978) used a conical net of 0.5 m diameter and 243 µm pore size to catch *Mysis relicta*, a mysid of similar adult length (Morgan, 1980). The base of my net was flattened to provide closer proximity to the substrate across most of the width of the net. This was necessary as *T. chiltoni* showed close association with the sediment surface and the deeper regions of the water column during daylight. The net was moved in 10 m sweeps between the marker stakes at an estimated velocity of 0.75 m sec^{-1}, which is close to the optimal mesh velocity for this mesh size (Tranter, 1968). The net opening was held perpendicular to the direction of water movement, to prevent abnormal current flow, and kept just above the substrate to avoid sediment blockage of mesh apertures. Mysids collected from each 10 m transect were fixed as a single sample when numerous, or as a sample representing a known number of 10 m transects when less abundant. An

attempt was made to collect at least 30 mysids at each station. Four percent formaldehyde was used as a fixative as it functions by precipitating soluble proteins (Steedman, 1976) causing deactivation of intestinal tract digestive enzymes if fixatives penetrate the digestive system effectively (Darnell, 1958) preventing further digestion of ingested materials. Food in the cardiac portion of the stomach of mysids is not mixed with the enzymes secreted by the hepatopancreas until it passes into the pyloric chamber of the stomach (Gelderd, 1909) and is then subject to digestive breakdown prior to enzyme deactivation. This partial digestion can cause some loss of recognisable characteristics in certain foods; however, as the pyloric chamber is noticeably smaller than the cardiac chamber in *T. chiltoni*, the majority of the food is unaffected. In case formaldehyde penetration failed to prevent further digestion, all mysid specimens were kept cool in the field and stored at 4°C upon return to the laboratory to further decrease catalytic effects.

2.2.4 Large Water Column Food Resources

The third sample collected was to evaluate potential animal foods present in the water column. It was collected using a 0.25 m diameter net of 100 µm mesh pulled upwind from and parallel to the mysid haul at the same depth and speed. A single 10 m haul was made at each station. The sample was fixed immediately in 4% formaldehyde.

The contents of nets used in mysid and large water column samples were individually washed into a plankton sorter to facilitate transfer to fixative vials.

2.2.5 Small and Large Benthic Food Resources

Two types of mud samples were taken from the top two centimetres of substrate in an undisturbed region of sediment. For the small benthic food resources sample three cores of sediment 2 cm deep were taken using a 5 c.c. hypodermic syringe with the nozzle end removed so that the barrel functioned as a corer. These cores were combined and preserved in sufficient 40% formaldehyde to make up a solution of 4% (not allowing for mineral grain displacement volumes). A second sample comprised three equal quantities of sediment to make a total volume of one litre of sediment collected using a rectangular container protruding 2 cm below a ski made out of moulded perspex sheet; this comprised the large benthic food resources sample for the site. The ski regulated the depth of the

sampler's blade, while the sides of the container functioned as a cutting edge. As more mud was cut, that already cut was pushed to the back of the container. The three samples were mixed together with 100 ml of 40% formaldehyde in a large plastic vessel. The three sub-samples of each benthos sample were taken from points equally spaced and adjacent to the sample transect used for the mysid net haul.

2.2.6 Dissolved Oxygen and Salinity

0.5 l of water was taken from each site to determine the salinity and approximate dissolved oxygen concentration. The bottles used were filled and sealed underwater (to prevent bubble formation and kept insulated in the dark to reduce errors in the determination of dissolved oxygen caused by photosynthesis and respiration.

Dissolved oxygen and salinity were determined immediately after returning from the field a few hours later. Dissolved oxygen was measured in the 0.5 l lake-water samples using a Y.S.I. Model 57 Oxygen Meter. The same sample was then analysed for salinity using a Y.S.I. Model 33 S-C-T Meter. The objective of measuring dissolved oxygen was to determine whether it was a factor limiting *T. chiltoni* distribution. As, even after storage as indicated, dissolved oxygen levels were consistently high, and did not appear to be limiting the distribution of *T. chiltoni* in this study, or of mysids in other studies (Mauchline, 1980) at the levels observed within Lake Ellesmere, it was not considered necessary to modify the method used.

2.2.7 Other Environmental Observations and Opportunistic Sampling

Determinations of water temperature (±0.25°C) using a mercury thermometer, turbidity (±5 cm) using a 10 cm white disc, and wave height (±2 cm) using a calibrated stick were made at each site. Wind strength and direction, water colour and light conditions were estimated. The above were recorded for each station, together with notes on observations of special interest.

Any fish netted were slit open just anterior to the anus and preserved in 4% formaldehyde; this treatment prevents further digestion subsequent to fixative penetration (Darnell, 1958). Possible food resources which were poorly sampled by the standard programme (e.g., epilithic diatom blooms) occasionally became apparent. Samples of these were collected, where this proved feasible, and preserved.

2.3 PREPARATION OF FIELD SAMPLES FOR MICROSCOPICAL EXAMINATION

2.3.1 General

On returning to the laboratory all samples were prepared for examination. The sequence of treatment was determined by the different materials' vulnerability to deterioration. Where a large amount of material was present in a sample fresh fixative was added before storage, as recommended by Steedman (1976). Material especially susceptible to biodegradation (i.e., *T. chiltoni* and fish digestive tract contents) was stored at 4°C prior to treatment. All samples were agitated to ensure penetration of fixative before storage.

2.3.2 Mysid Samples

Next morning each sample of mysids was removed from the refrigerator immediately prior to analysis. Determination of species, size and sexual grouping, and dissection of 30 mysids from each site, normally took two days to complete with a maximum of four days for the sample collected in November 1979 when the population was at the minimum modal length recorded during this study and required extreme care during dissection.

Each sample was placed in a Petri dish and the mysids hand-sorted into a second Petri dish. The remaining material was checked for any further mysids under a dissecting microscope at a magnification of 63x. The sorted sample was then counted. If 30 or fewer specimens were present, the entire sample was put into 70% ethyl alcohol for later dissection, otherwise 30 specimens were selected randomly and placed in 70% ethyl alcohol. These specimens were than removed individually and put through the sequence of procedures described below.

(1) The length of each mysid was measured as the distance separating the tip of the rostrum from the tip of the telson to the nearest 0.5 mm as used by Brattegard (1969), which, for *T. chiltoni*, closely approximates length as defined by Mauchline (1970) and is a measure of the Total Length of a mysid (Mauchline, 1980).

(2) Sexual development was determined using the sexual stages defined by Mauchline (1968). Individuals were classified as neuter, immature male, mature male, immature female, mature female bearing young or mature females not bearing young; which correspond to Mauchline's (1968) stages 1 to 6.

(3) Mature females bearing young had embryos removed from the marsupium; these were counted and classified as "eggs", eyeless larvae or eyed larvae, corresponding to stages I to III respectively of Mauchline (1980).

(4) A subjective assessment of stomach fullness was made from 0 (empty) to 4 (full) with five equal intervals, and the stomach colour and colour intensity estimated.

(5) A more objective measure of feeding success was made from 0 (0-20% full) to 4 (80-100% full) by measuring the length of the intestine behind the posterior end of the dorsal surface of the carapace and comparing this length with the length of intestine containing partially digested material. This was called the intestinal fullness index.

(6) The mysid was identified using the criteria given by Chapman and Lewis (1976) to distinguish *T. chiltoni* from *T. novaezelandiae*.

(7) The specimen was dissected to remove the stomach and its contents. Great care was taken to avoid spillage of stomach contents during dissection. The entire stomach was removed with the oesophagus and some of the intestine attached. Once dissected out of the mysid, the oesophagus was dissected away and the intestine cut posterior to the dorsal diverticulum. The stomach was then placed in a clean transparent plastic vial containing 10 ml ethyl alcohol. An incision was made along the length of the stomach through the walls of both cardiac and pyloric chambers. The stomach was then sealed in the vial. All vials were labelled and stored until all selected specimens had been processed for that sample period.

(8) Each stomach was then subjected to 15 seconds ultrasonic treatment of 25 watts intensity. If aggregated manducated material was still visible within the chitinous stomach wall it was given a maximum of three further 5-second ultrasonic treatments after making a further incision in the stomach wall. Less than 20% of any one month's stomach samples required more than 15 seconds in the ultrasonic bath.

(9) The material was then prepared for microscopic examination modifying the technique of Cummins (1973) by substituting Gelman Instrument Co. Metricel G.A.6 0.45 μ filters and lactophenol P.V.A.

as a mountant. To partially offset the large difference in volume of food ingested which was expected between the largest and smallest specimens, three different sizes of adaptor funnels were used to condense the ingested material further than a standard 22 mm diameter Millipore funnel permitted. These adaptor funnels condensed the material onto filter discs of 4.0, 5.5 and 8.5 diameter and were used for stomach contents from mysids in the length ranges of 2.0 - 7.0 mm, 7.5 - 12.0 mm and 12.5 - 17.5 mm, respectively. The use of Gelman 0.45 µ filters and lactophenol P.V.A. mountant necessitated a 24-hour clearing period, protected from dust, prior to putting cover slips over the material.

2.3.3 Food Resource Samples

The small water column food resources samples were filtered individually. The sample was well mixed and 11 ml (10 ml lake-water and 1 ml 40% formaldehyde) pipetted into the filter column. After filtration onto a 22 mm diameter disc of HA 0.45 µm membrane filter, the filter was dried in air, cleared with immersion oil and mounted on a slide. No further processing of the large water column food resources samples was required prior to analysis.

The small benthic food resources samples were chemically cleaned of organic matter using the technique of Swift (1967), leaving only sediment grains, diatom frustules and other stable mineral structures. This residue was then made up to 60 ml with distilled water. The sample was resuspended by agitation and 5 ml pipetted into a 22 mm diameter Millipore filter column and filtered through HA 0.45 µ membrane filter. The filter was air dried, cleared in immersion oil and mounted on a slide.

The large benthic food resources samples were separated from the sediment contained in each sample using Mr G. Fenwick's modification of the Whitehouse and Lewis (1966) flotation technique (pers. comm.), which substitutes kerosene for carbon tetrachloride as the organic flotation agent. The initial volume of the sample was recorded. To assist sorting animal material from filamentous algae and macrophyte detritus, the separated sample was then counterstained for high colour contrast using the technique of Williams and Williams (1974).

2.4 MICROSCOPICAL TECHNIQUES

2.4.1 Identification of Foods

Before accurate counting of the foods ingested was possible, it was necessary to identify all possible food species or groups. As the ultimate objective was the recognition of particles ingested by *T. chiltoni*, systematic classification was not normally attempted beyond the limits imposed by the effects of mastication and partial digestion by the mysids, microscopical preparation and resolution of the techniques used.

Collections of diatoms, pipetted from settled lakewater samples and from the digestive tracts of mysids, were acid-cleaned using the technique of Weber (1966) and were dehydrated using a series of ethyl alcohol solutions. The diatoms were then filtered onto Millipore HA 0.45 µm filters, critical point dried and prepared for observation under a Cambridge 600 Scanning Electron Microscope. The micrographs obtained were used to identify diatoms to the generic level where possible. Identification was undertaken with the assistance of Cassie (1980); Chapman, Thompson and Segar (1957); Cleve-Euler (1951); Crosby and Wood (1959); Flint (1966); Foged (1979); Sarma and Chapman (1975); Taylor (1970) and Wood (1960, 1963). An atlas of diatom frustules was compiled to assist in diatom identifications during the study. Due to the lower resolution of the light microscopes used, and the impossibility of using optimal diatom techniques (detailed in Hasle and Fryxell, 1970; Sterrenburg, 1978) when organisms identified by the morphology of soft structures were also present within a sample, diatoms could not always be identified to genera. Groups were erected, therefore, on the basis of diatom similarity under prevailing experimental conditions. Diatom groups were counted as whole cells, or quarter valves where the frustule proved prone to fragmentation (see Table 1 for details). Filamentous algae were not identifiable further as the filaments were frequently ruptured during mastication and partially desiccated during preparation destroying characteristic structures. Filamentous algae were classified, therefore, as a single group and counted as the number of 62.5 µm grid length sections of filament present.

Spores derived from algal (and some hyphal) filaments were present in the stomach contents in small numbers. The phylogenetic origins of these spores were not normally ascertainable. A spore was counted as a single unit and sometimes shown to be derived from a filamentous alga.

Table 1. A summary of the relationships between the systematic classification of the bacillariophyceae and the diatom groups used in this study.

Diatom group	Sub-Classification (if any)	Genera contained within group	Members of contained genera previously recorded from L. Ellesmere
A	Pennates, >50 µm	*Cymbella, Synedra*	*Cymbella ehrenbergii, Synedra tabulata, S. ulna, S.* sp.
B	Pennates, 20-50 µm	*Cymbella, Diatoma, Licmorphora, Synedra*	*Cymbella ehrenbergii*
C	Pennates, <20 µm	*Amphora, Mastogloia,*	*Amphora terroris, A. turgida, Mastogloia angulata, M. braunii, M. cribrosa, M. pumila*
D		*Cocconeis*	
E		*Achnanthes*	*Achnanthes coarctata, A. exilis*
F	Centric, >50 µm	*Coscinodiscus, Cyclotella*	*Coscinodiscus* sp., *Cyclotella* sp.
G	Centric, <50 µm	*Chaetoceros, Sceletonema?*	*Chaetoceros* sp.
H		*Biddulphia*	
I		*Campylodiscus*	*Campylodiscus* sp.
J		*Hyalodiscus*	
K		*Gyrosigma, Nitzschia?*	*Nitzschia acicularis, N. closterium, N. graeffii, N. sigma* var *rigida, N.* sp.
L		*Amphora?, Diploneis, Navicula, Surirella*	*Surirella striatulata, S.* sp.

Single-celled and multicellular planktonic or benthic chlorophytes made up a small volume of the diet of *T. chiltoni*. They were normally ruptured during ingestion, losing the fine structure required for further identification. A count was made of the number of cellular units present.

The origin of plant detritus was identifiable in less than 1% of observations made of ingested material. The great majority of plant fragments were from monocotyledons, where identifiable, and were probably principally derived from the various species of grasses bordering the lake. Plant detritus was therefore ascribed to a single group for the purpose of enumeration and counted as the total number of 62.5 µm search grid squares filled within each field of view. Where possible the origin of plant detritus was noted.

Mineral material was rare in stomach contents and generally associated with the ingestion of larvae of *Chironomus zealandicus*. It was considered an insignificant source of energy and ignored.

Possible crustacean prey were initially identified, where possible, from Chapman and Lewis (1976). The identifications were confirmed by reference to Bayly, 1963 (*Gladioferens pectinatus*); Chapman, 1963 (*Gomphocythere duffi* and *Cyprinotus flavescens*); Hurley, 1954 (*Paracorophium lucasi*) and Barnard, 1972 (*Paracalliope fluviatilis*). Dr M.H. Lewis of the University of Auckland identified two species of harpacticoid copepods as *Braniola canterburyensis*, a new species, and *Tachidius* sp. closely resembling *T. incisipus* (pers. comm.). *Gomphocythere duffi* and *Cyprinotus flavescens* are new additions to the list of fauna and flora given in Hughes *et al.* (1974). The other crustacean found, *Austridotea annectens*, was infrequently ingested and its identity was not confirmed by reference to original papers.

The only species of insect of consequence to the study was *Chironomus zealandicus*, whose identity was confirmed by J.D. Stark, University of Canterbury. A single specimen of another chironomid species was found but not identified.

Some other vertebrate and invertebrate species were present in moderate numbers at Timberyard Point. These will only be commented upon briefly in Chapter 5 as they contributed little or nothing to the diet of *Tenagomysis chiltoni*.

Two reference collections of all the above possible food species were established. The first collection was preserved intact. In the

second collection selected specimens were dissected to remove appendages for mounting in lactophenol P.V.A. with lignin pink added. The remainder of the second collection was subjected to ultrasonic bombardment for one minute. The resulting fragments were collected on a Millipore HA 0.45 µm filter which was partially cleared with lactophenol P.V.A. with lignin pink added. The ultrasonic fragmentation technique, developed for this study, produced a similar range of fragments to the range of fragments produced when *T. chiltoni* masticated small crustaceans. Dissection gave better results than ultrasonic fragmentation for crustaceans larger than 2 mm in their maximum dimension. Ultrasonic fragmentation was a useful supplement to manual methods as a means of obtaining fragments of smaller organisms such as Copepoda and Ostracoda.

To ensure accuracy of counting in the determination of *T. chiltoni* stomach contents, three mixtures of organisms were prepared and the contents recorded by a second party, the contents being unknown to the experimenter. After ultrasonic fragmentation and slide preparation the fragments were enumerated to reproduce the original sample composition.

The stomachs of a number of mysids were examined to select animal fragments produced by natural mastication which were suitable for use as Count Indicator Particles. The criteria used for the selection of the Count Indicator Particles were:-

(i) the particle must be of distinctive appearance;
(ii) the particle must be relatively stable during mastication;
(iii) the number of particles derived from each individual of a species should be constant, if possible, and as large as allowed within the confines imposed by the other criteria;
(iv) the particle must readily detach from the main body of the animal; and
(v) the particle must be sufficiently small to pass through the stomach filter of *T. chiltoni* without even temporary retention, avoiding the effects of gut passage time differences between different food particles.

A list of the Count Indicator Particles selected for each animal commonly occurring in the diet of *T. chiltoni* at Timberyard Point is given in Table 2.

Table 2. Principal dietary components, counted units and calculated food volumes.

Food and count particle description			Number of counted units per organism or particle of food	Calculated volume of whole organism or particle (μm^3)	Calculated volume of food ingestion represented by a single counted unit (μm^3)
Broad taxonomic grouping	Specific name or description	Counted unit			
Bacillariophyceae	Diatom Group A	Complete frustule	1	3 682	3 682
"	" " B	" "	1	755	755
"	" " C	" "	1	77	77
"	" " D	" "	1	627	627
"	" " E	" "	1	12 034	12 034
"	" " F	Quarter valve	8	532 696	66 587
"	" " G	Complete frustule	1	1 355	1 355
"	" " H	" "	1	13 431	13 431
"	" " I	Quarter valve	8	199 264	24 908
"	" " J	" "	8	360 752	45 094
"	" " K	Complete frustule	1	13 700	13 700
"	" " L	" "	1	10 360	10 360
Chlorophyceae	Filamentous algae	62.5 µm lengths	Variable	Variable	48 143
"	Unidentified spores	Cellular units	1	1 103	1 103
"	Microscopic chlorophytes	" "	1	1 936	1 936
"	Plant detritus	62.5 µm grid squares	Very Variable	Very Variable	56 024
Crustacea, Copepoda	Adult *Gladioferens pectinatus*	(terminal segments of urosome and outer leg of pair)	12	2 346 864	195 572
" "	Juvenile *G. pectinatus*		6-12	945 972	105 108
" "	*Branicla canterburyensis*	As *G. pectinatus*	12	1 114 068	92 839
	Tachidius (incisipus?)	As *G. pectinatus*	12	2 384 772	198 731
Crustacea, Ostracoda	*Gomphocythere duffi*	Antennae, antennules and legs	10	501 390	50 139
Crustacea, Amphipoda	*Paracorophium lucasi*	Gnathopod and pereiopod claws	14	Claw length regression equation used	
Insecta, Chironomidae	*Chironomus zealandicus*	Mandibles	2	Mandible length regression equation used	

The level of counting necessary to produce statistically acceptable stomach content data was determined using data from the stomach contents of 15 mysids (5 neuter, 5 male, 5 female). The mysids were 7.5 - 13.0 mm long and collected in February 1980 from site 3. The contents of 20 fields of view on the prepared filter were determined using a Nikon Biophot microscope fitted with a Carl Zeiss "Neofluar" 16/0.40 phase contrast objective. The effective magnification of the system was 240x. Data obtained were analysed using a nested Analysis of Variance program. Calculated between specimen and between replicate variances were used in equations given in Snedecor and Cochran (1967) to solve for the required number of subsamples. The analysis suggested that counting 10 fields of view would give a standard error of about 6%.

2.4.2 Mysid Stomach Content Analysis

The contents of a total of 1114 stomachs of *Tenagomysis chiltoni* were prepared for examination using the above techniques. The items present within each stomach were evaluated by counting ten adjacent fields of view along a transect crossing the centre of the filter disc of ingested material. A summary of the counted food items and associated data is given in Table 2. Diatom groups A to L, algal filaments, spores, microscopic sphaeroid chlorophytes, plant detritus and all animal Count Indicator Particles were enumerated. *Gladioferens pectinatus* fragments were classified as of juvenile or adult origin on the basis of leg structure. Tarsal claws of amphipods and mandibles of chironomids were measured to the nearest 5 µm. Notes were taken of any unusual objects or observations, and photographs were taken where appropriate.

2.4.3 Food Resource Evaluation

A count was made of all materials from the four types of food resource samples shown to be ingested by *T. chiltoni*. Over 200 specimens were counted from each sample of the two categories of large foods resources and over 150 specimens from each category of small foods resources sample. Lund, Kipling and Le Cren (1958) stated that a count of 100 algal cells was "normally safe" at ±10% error. Dr R.M. Cassie (in Edmondson and Winberg, 1971) stated that if the distribution was Poisson and the count was over 100 units then the coefficient of variation was less than 10%. The filter technique used for the small foods resources samples should produce a distribution closely approximating a Poisson distribution. The

Petri dish technique used for the large foods resource samples should produce a close, but less perfect, approximation to a Poisson distribution. In view of the time limitations imposed upon the project it was not practicable to apply stratified sampling techniques to determine specimen distributions in the field. It is, however, now recognised that count statistics derived from material collected in the present study would be preferable to those used.

The number of fields examined and the area covered by a sample were recorded. These values were later used to standardise the abundance data, obtained during counting, into numbers representing the absolute abundance of each resource. This procedure allowed combination of small and large foods resource data to form composite Water Column and Benthic Food Resource data, representative of the potential available foodstuffs defined as foods occurring within a habitat which were available for consumption by an organism (Berg, 1979).

2.4.3 (a) Water column food resource counts

A count was made of all diatom groups, algal filaments, spores, ingested forms of chlorophytes and plant detritus on adjacent fields in a transect across the centre of the filter of each small water column food resources sample. All recognised types of count units within each field of view, including the final field of view, were counted until the total count exceeded 150 units. The number of fields examined was recorded. Counts were made under the same microscope and conditions as for the evaluation of stomach contents.

A count was then made of all species of animals in each large water column food resources sample. The individual samples from each site and sampling period were allowed to settle in a Petri dish mounted on the moving stage of a Leitz Diavert inverted microscope. Adjacent fields of view were counted until the total count exceeded 200 animals, using a Leitz planar 2.5/0.08 objective and GF 12.5x eyepieces giving a magnification of 31.25. The number of fields examined was recorded.

(b) Benthic food resource counts

As the small benthic foods resource samples had been chemically treated to remove soft tissues, only those potential food items having resistant hard parts remained. This residual fraction consisted principally of diatoms. The count was made as for the small water column

foods resource samples except that only members of different diatom groups were counted.

The large benthic food resources count was made in an identical manner to the large water column food resources count except that algal filaments, spores, chlorophytes and macrophyte detritus had to be evaluated from these samples as they had been chemically removed from the small benthic food resources samples.

2.5 NUMERICAL AND VOLUMETRIC METHODS

2.5.1 Methods of Calculating Various Population Parameters Used in the Study

The numbers of mysids per 10 m haul were determined for each sampling station for each sample collection date. Subsequently, a mean numerical density for each sampling period was calculated giving equal weight to each station, even when mysids were absent at some stations. The numerical abundance of mysids of successive times was used to calculate the Population Growth Index over each period.

The principal methods of analysis of the population structure have been detailed previously (p. 10). The determinations of the length, sex, brood size and embryonic stage for the four sampling stations were pooled for each sampling period, giving a maximum sample size of 120 specimens for any sampling date. Neuter individuals under 3 mm in length were only counted if they showed evidence of active feeding, as Wittman (1978) demonstrated natural marsupial loss of larvae.

Combining the results from all sampling stations increased count consistency and dampened the effects of local variation in population structure, found in this study and also those of Clutter (1969) and Mauchline (1970a).

Specimens from each sampling period were divided into 1 mm size groups and segregated according to the secondary sexual development shown by each specimen. The number of specimens of the same size and sex was calculated, and plotted as a percentage of the total number of specimens classified and dissected from all stations in that month. The histograms constructed from these data were used to determine the population changes during a single annual cycle from September 1979 to October 1980.

An overall male : female ratio was calculated from the numbers of all individuals showing male or female characteristics in each sampling period. An adult male : female ratio was calculated in an identical manner using only data for fully mature individuals.

2.5.2 Aboslute Abundance Calculations for Evaluation of the Food Resources

From knowledge of the volume of lake water or sediment processed to extract a sample, the area of the filter or Petri dish over which a sample was distributed during examination, the area of that sample examined (the number of fields examined multiplied by the area of each field), the count made of any one particle type and a number of calculated constants, the absolute abundance of that particle type can be determined. For any sample distributed on a two dimensional surface during examination the absolute abundance of any particle of type x can be calculated from the equation:

$$N_x = \frac{A_t \cdot C_x}{A_e \cdot V}$$

where N_x = the number of particles of type x per litre of fluid.

A_t = the total area covered by the sample being examined (mm^2).

A_e = the area of the sample examined (mm^2).

C_x = the count of particle type x from within A_e.

V = the volume of fluid (excluding fixatives) processed (litres).

In cases where a net was used to collect a sample (large water column food resources samples) the net is assumed to be 85% efficient. 85% is the lowest acceptable operational filtration efficiency of plankton nets (Tranter, 1968). N_x is therefore multiplied by the resulting net efficiency factor of 1.176 in such instances.

2.5.3 Food Volume Calculations

As a first approximation to the potential nutritional value of different food resources and dietary components all data were mathematically transformed from a numerical form to volume approximations. Each significant item of the diet was measured to determine the dimensions necessary to calculate displacement volumes for the geometrical form which

the item most closely approached in three dimensional structure. The most appropriate equations for the calculation of displacement volumes of the food types present were selected from Gellert, Kustner, Hellwich and Kastner (1977) by Mr K.W. Duncan (Table 3). Measurements compatible with the appropriate displacement volume equation (see Table 3) were made from 40 specimens of the most common food types, 25 specimens of frequently ingested particles, 10-15 specimens of moderately common food items and 5 specimens of those foods consumed infrequently.

The heights of microscopic food items were measured at high magnification using a calibration of markings on the fine focus control of the microscope made using the depth of a cover slip as an item of known depth; other height measurements were made by rotating the specimens on the stage of an inverted microscope and using a calibrated graticule. All other measurements were made using calibrated graticules. Displacement volumes of amphipods and chironomids were calculated using model 2 regression equations of volume against tarsal claw length and mandible lengths respectively. Computations of mean particle volumes, standard deviations and standard errors for other food types were made using Fortran programs written by Mr K.W. Duncan. Mean displacement volumes of foods seldom ingested were calculated using an electronic calculator. The volume of the whole organism or particle was then divided by the number of counted units per whole organism or particle to produce a volume conversion factor (Table 2).

An ALGOL 60 program was written to calculate the total volumes, mean volumes and percentages of foods of each type present in the stomach of every specimen belonging to different groups (e.g., length groups or sexual groups) using a mathematically defined prescribed variable. This variable was used to separate the foods ingested by specimens into groups on the basis of mysid length, sex, stomach feeding index, intestinal feeding index, locality of collection, time of collection or an interaction of locality and time of collection. The program adjusted the weighting of foods of all types according to the mean population density of mysids at the time of sampling (to correct for size-specific volume differences in ingestion around the annual cycle) and also compensated for differences in the proportion of the filter inspected and filters of different areas. Calculated volumes were summed in groups defined by month, site, month and site, size, sexual grouping, stomach and intestinal feeding indices. Up to 44 groups could be defined each time the program was run. After

accummulating food volume totals for each of the 1114 specimens the total volume, percentage of the total volume of food and the mean volumes ingested per specimen were calculated for each food type. Food groupings were then defined on the basis of phylogenetic relationships, size or the food resource a food occurred within, and total volume and percentages calculated for each food group.

The ALGOL 60 program used to calculate dietary volumes was modified to calculate the volume of tissue contributed by the components of each food resource and percentages of each item of the diet from a data file similar in structure to the data file detailing the individual characteristics of the mysids examined during this study and the contents of their stomachs.

Table 3. Equations used in the calculation of food particle volume transformations for whole organisms or particles. H, height of a non-cylindrical solid; h, height of a cylinder; L, length; Q, segments width; r, radius; V, calculated volume; W, width; and π is equal to 3.14159265 for the purposes of calculation herein.

Geometric shape of organism or particle	Volume calculation equation	Food organisms or particles to which the equation was applied
Tabuloid	$V = L \times W \times H$	Diatom group E, macrophyte detritus.
Cylinder	$V = \pi r^2 h$	Diatom groups F, H, and I; Algal filaments, *Chironomus zealandicus*.
Sphere	$V = \frac{4\pi r^3}{3}$	Unidentified spores, microscopic chlorophytes.
Double identical segments of sphere	$V = \frac{\pi H(3Q^2+H^2)}{3}$	Diatom groups G and J.
Sardine can, elliptical in section	$V = \frac{\pi LWH}{4}$	Diatom groups A, B, C, D, K and L.
Single ellipsoid solid of rotation	$V = \frac{\pi LH^2}{24}$	*Gomphocythere duffi*, *Paracorophium lucasi*
Ellipsoid solid of rotation with atta ched cylinder	$V = \frac{\pi LH^2}{24} + \pi r^2 h$	Adult *Gladioferens pectinatus*, juvenile *G. pectinatus*, *Braniola canterburyensis*, *Tachidius (incisipus?)*

CHAPTER 3

POPULATION DYNAMICS OF *TENAGOMYSIS CHILTONI* IN LAKE ELLESMERE

3.1 INTRODUCTION

The biology of the majority of the some 765 known members of the Order Mysidacea is still largely unknown (Mauchline and Murano, 1977). Within the genus *Tenagomysis*, no investigations of seasonal changes in abundance, growth or population structure have been published.

The majority of the mysid species investigated have extensive breeding seasons which can partly obscure the distinction between different cohorts within a population, and no method of determining the age of individual mysids is available at present (Mauchline, 1980). However, most investigations have shown clearly defined length groups produced by differences in development between cohorts. Considerable size variation is apparent within the Mysidacea (Tattersall, 1955). Mature adult body length ranges from about 2.5 mm (*Anisomysis tattersallae* Pillai) to 350 mm (*Gnathophausia ingens* (Dohrn)), however adults of most species are less than 25 mm in length (data from Mauchline and Murano, 1977). *Tenagomysis chiltoni* adults ranged in length from 9.0 - 16.9 mm in males and 10.5 - 17.9 mm in females. Sexual development of mysids is defined by secondary sexual characteristics (e.g., Morgan, 1980), and is used, along with length, in the determination of generation histories. Mauchline (1980) recognises six types of life history defined on the basis of the rate of alternation of generations. The number of cohorts produced by a species within a given period may vary between different environments (Lasenby and Langford, 1972; Morgan, 1980). *Tenagomysis chiltoni* has at least two and probably three or more cohorts a year in Lake Ellexmere and is therefore probably in category E of Mauchline (1980).

The numerical abundance of most species of mysids fluctuates seasonally in a regular manner, the principal cause of these fluctuations being the seasonal reproductive pattern of the population (Mauchline, 1980). The exact nature of these oscillations in mysid population density, and associated changes in length composition of a population are of interest in the study of foods ingested by mysids (Kost and Knight,

1975; Rybock, 1978; Siegfried and Kopache, 1980), and of predation upon mysids (Sitts and Knight, 1979). Variation in seasonal mysid population fluctuations are dependent on species (Mauchline, 1971c), latitude (Mauchline, 1980), water temperature (Lasenby and Langford, 1972; Modlin, 1979; Tattersall, 1955), locality (Borghouts, 1978; Morgan, 1980) and may also depend on nutrient constraints (Cushing, 1959; Morgan, 1980; Olsen, 1980). Brood size is correlated with length of parent (Borghouts, 1978; Clutter and Theilacker, 1971; Hakala, 1978; Mauchline, 1967, 1969, 1971a, b, 1980), which will be partly dependent on the food ingested. The size composition and numerical abundance of the population of *T. chiltoni* can be expected to influence the quality and quantity of food ingested by the population, and in turn to be affected by the quantity and quality of the food. The examination of these interrelationships is therefore an integral component in the study of mysid feeding.

3.2 RESULTS

3.2.1 Population Densities

The mean number of specimens captured in a 10 m net haul was 45 on 26 September, 1979 (Fig. 2a) and by 8 November the population had increased slightly. Between November 1979 and mid-January 1980, rapid recruitment occurred as both overwintered and spring generation adult females released their broods so that the population reached its maximum recorded density (236 individuals/10 m) in January. Between 14 January and 6 May 1980 mortality exceeded recruitment, causing a rapid decline in population numbers. In mid-March the population density was similar to the population density at the start of the study. After March the population showed a slower but consistent decline in numbers, except in June when the previously high salinity conditions ended (Fig. 2b), during the autumn and winter months until by 4 October 1980 (the last sample collection date of this study) the population had reached a density of four specimens/10 m, the lowest mean density recorded during the sampling programme. This figure is only 8.2% of the initial mysid population density and 1.6% of the maximum observed mysid density.

The period of maximum population recruitment corresponds to the spring increase in water temperatures and increases in the volumes of food present in the stomachs of mysids. The maximum rate of population decrease is coincident with the maximum observed salinity level created

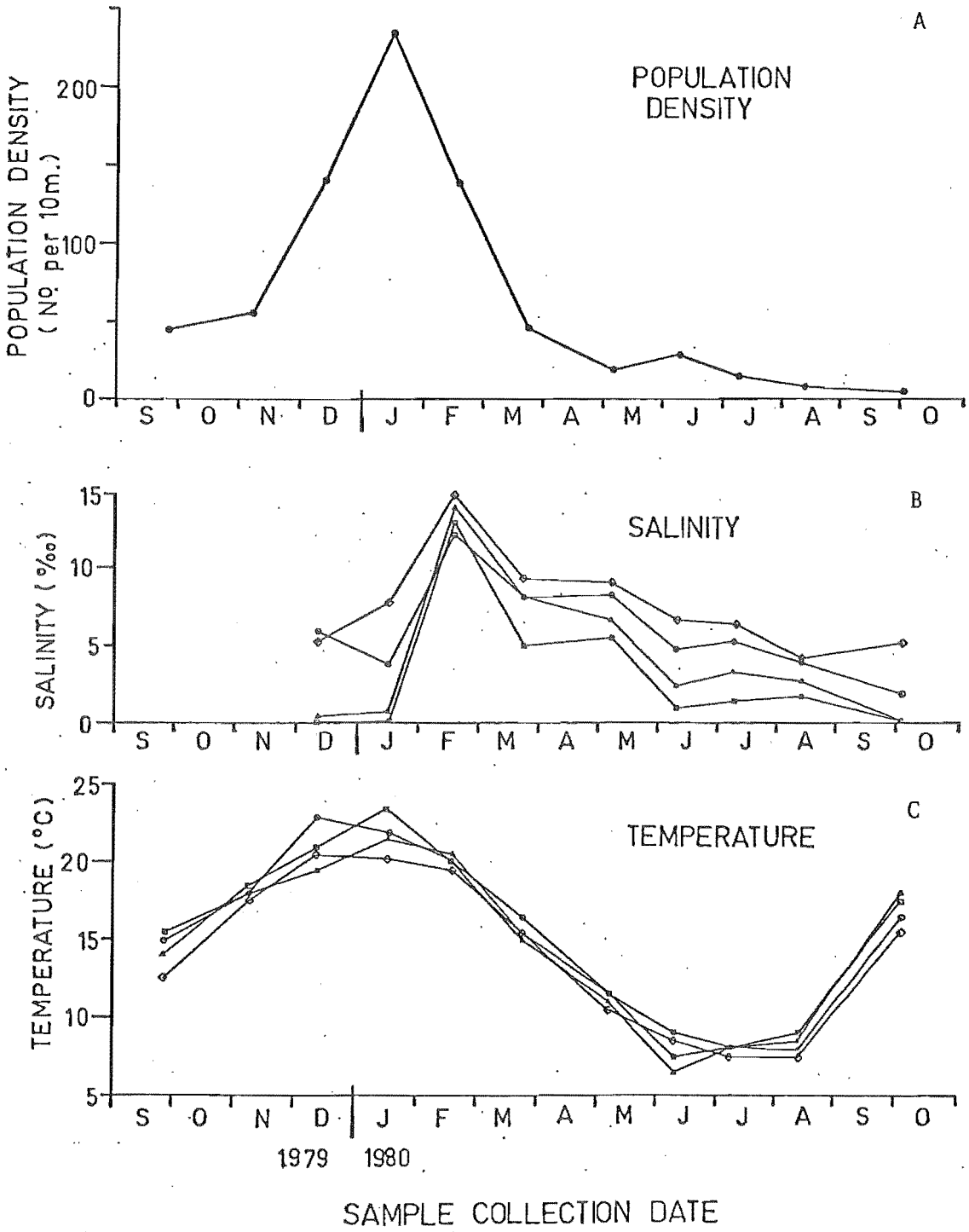

Fig. 2 Seasonal variation in the abundance of *Tenagomysis chiltoni* (Graph A), salinity (Graph B) and water temperature (Graph C) in the study area. Hollow squares = Site M, hollow triangles = Site 1, hollow circles = Site 2, hollow diamonds = Site 3, solid circles = all sites combined.

by abnormal conditions during the period when the lake was open to the sea and is not related to successional changes in the population of *Tenagomysis chiltoni*.

Mean population densities at each site, over all sampling periods, were 40, 84, 88 and 54 mysids/10 m at sites M, 1, 2 and 3 respectively. Site to site variation in population density was not significant at the 75% level (One-way ANOVA : F = 0.455, df = 3/40, p = 0.2748).

3.2.2 Population Structure and Succession

The population showed marked successional changes which exerted a strong influence on the size distribution and abundance of *Tenagomysis chiltoni*. There were two distinct periods of reproductive activity, during the spring and summer, which overlapped slightly, and probably an autumn cohort partly obscured by overlapping size classes of different cohorts, followed by an extended period of sexual quiescence over the winter months.

The first samples used in this study were collected on 26 September 1979. At this time individuals within the population had a total length of from 8.0 - 17.5 mm (Fig. 3). Sixty-three individuals showing female sexual characteristics had a mean length of (13.4 mm, 1.3 mm longer than the 36 specimens exhibiting male secondary sexual characteristics. The overall male:female ratio was 0.57. Twenty-one neuter specimens ranged from 8.0 - 11.5 mm in length, noticeably shorter than most mysids showing external sexual development. Numerous sub-adults of both sexes were present. All but one specimen showing adult female characteristics in the brood pouch structure were actively breeding in September. No sexually reproductive females were found in two samples of 30 mysids collected near Lower Selwyn Huts in mid-August 1979. The maximum length of eyed larvae (Stage III of Mauchline, 1980) present in the brood pouch of reproductive females at any time during this study was 2.1 mm. No mysids present in the September sample were less than three times this length, therefore adult females were not yet releasing post-larvae.

By 8 November a marked change had occurred within the population (Fig. 3). The large number of sub-adult males and females present in September had almost disappeared, only three sub-adult females being present. A moderate number of adults of the overwintering population remained (overall male:female ratio 0.105), but the whole overwintering population was now less than 10% of the overwintering population level

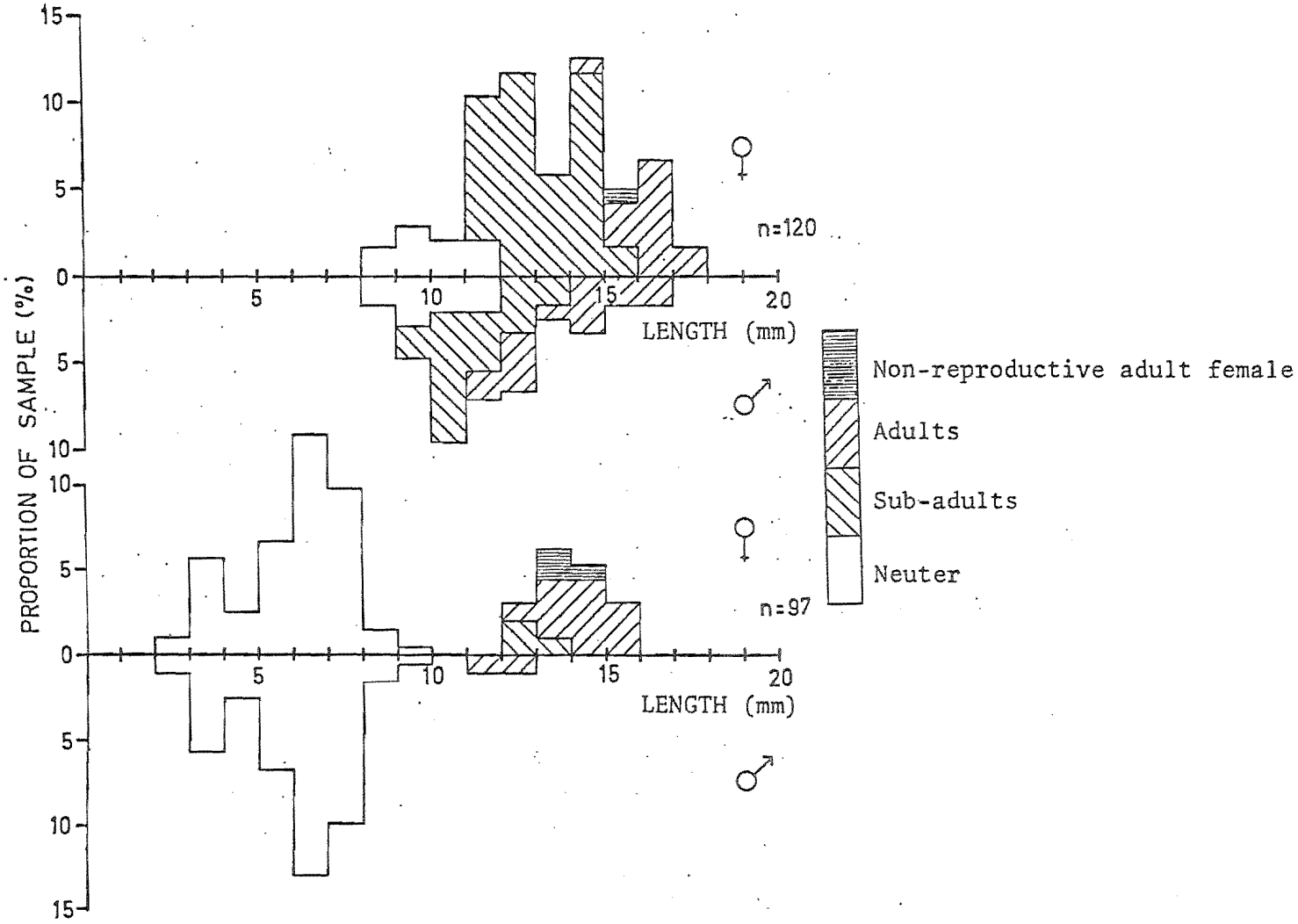

Fig. 3 Population structures sampled 26 September 1979 (top) and 8 November 1979 (bottom). Neuter specimens are plotted symmetrically about the X axis, females above the X axis, males below the X axis.

in September (after correction for differences in relative abundance of mysids between the two periods). 2 mm in total length (when analysed in 0.5 mm size groups) separated the overwintering group from a smaller spring generation produced by the now declining overwintered population. This spring generation comprised over 80% of the total population and ranged from 2.5 - 9.0 mm in length with a modal length of 6 mm which represents a modal growth of 4 mm or a trebling of total length from the 2.1 mm eyed larvae in less than 44 days which elapsed since marsupial release. There was no evidence of maturation of this spring generation in the development of either primary or secondary sexual characteristics.

By 11 December 1979 (Fig. 4) the overwintering population was still evident as a small group of fully mature adults (overall male: female ratio 0.166), but only 7.8% of the numbers present in September remained. This group was now separated from the spring generation by 1.5 mm in length. The spring generation ranged from 2.5 to 12.0 mm in length with a modal length of 10 mm, and showed evidence of decreased recruitment in the shorter length groups. The spring generation also showed marked sexual development. Sub-adult and fully adult mysids were present in three samples (overall male:female ratio 0.72), and the largest fully adult females carried broods. Sexual development was both initiated and completed while individuals were approximately 2 mm shorter than corresponding male and female groups of the overwintered generation. Most neuter specimens had a total length of less than 10 mm. At this time the population showed rapid increase in numbers.

The samples collected on 14 January 1980 contained no apparent remnants of the overwintering generation (Fig. 4) and the maximum size of the spring generation individuals had not increased (which could have obscured the presence of larger overwintered adults). A marked increase in recruitment to the population was apparent, contributed largely by the sample collected from Station 2. The length frequency structure of the spring generation was basically similar to that of the December sample, except that a larger proportion of sub-adult females was present. The overall male:female ratio had fallen to 0.55. Mean water temperature was now 21.4°C, the maximum recorded for the year.

On 19 February there had been very little recruitment of small mysids in spite of the presence of a large number of actively reproducing females (Fig. 5). In these four samples mean length of males was 9.7 mm which is 2.4 mm shorter than in September 1979. The mean length of females was 11.2 mm, 2.2 mm shorter than in September 1979, and 1.5 mm

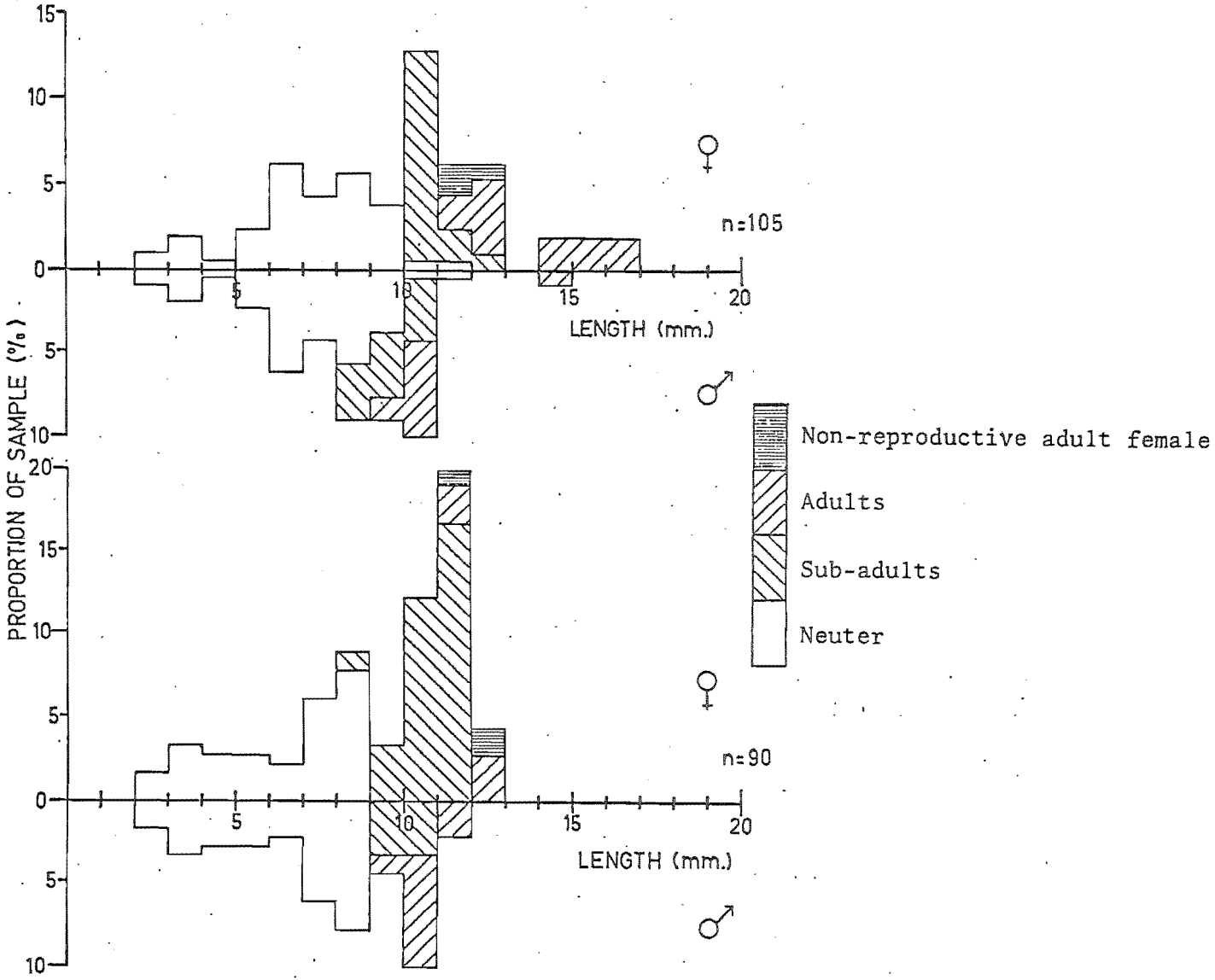

Fig. 4 Population structures sampled 11 December 1979 (top) and 14 January 1980 (bottom). Neuter specimens are plotted symmetrically about the X axis, females above the X axis, males below the X axis.

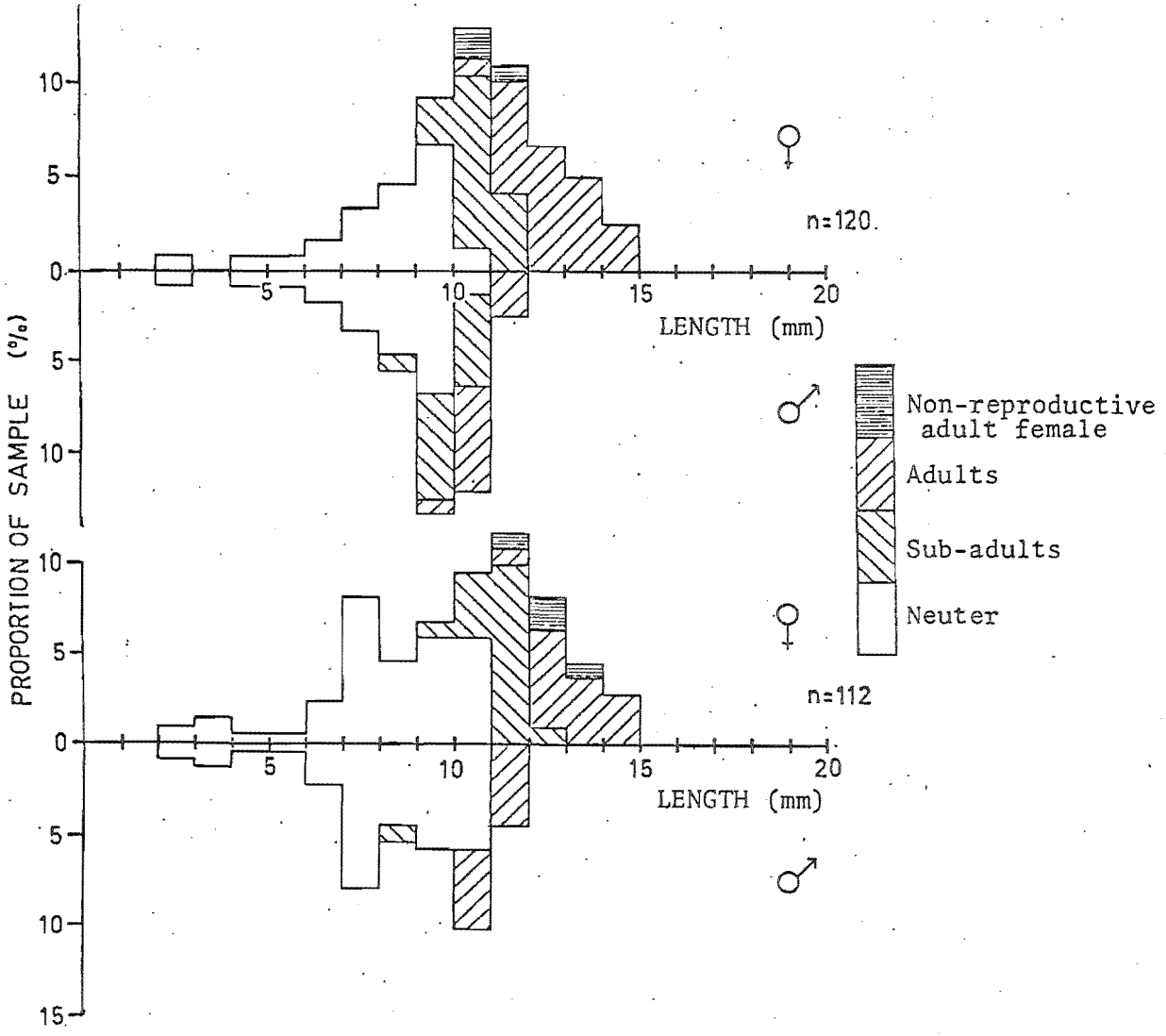

Fig. 5 Population structures sampled 19 February 1980 (top) and 23 March 1980 (bottom). Neuter specimens are plotted symmetrically about the X axis, females above the X axis, males below the X axis.

longer than the mean length of males compared with 1.3 mm in September 1979. Most of the population were from 7.0 to 14.0 mm in total length, with a modal length of 10 mm. The ranges of length exhibited by each sexual group were:- Neuter, 2.5 - 10.0 mm; Sub-adult Male, 8.5 - 10.0 mm; Adult Male, 9.5 - 11.0 mm; Sub-adult Female, 9.5 - 11.5 mm and Adult female, 10.5 - 14.0 mm. The overall male:female ratio was 0.53.

On 23 March (Fig. 5) there had been little change in the population except that the 6 - 11 mm size groups showed a smaller modal size and less sexual development in comparison with the February samples. This apparent shift may have been a random sampling error rather than real. Minimal recruitment of males from the neuter group was evident. The overall male:female ratio had decreased to 0.31. However, the overall male:female ratio dropped further to 0.29 and 0.27 in May and June respectively, although moderate to high adult male recruitment was evident. Moderate numbers of adult females, the majority carrying broods, were present. Recruitment of young was small but consistent within the 2 - 5 mm length groups.

By 6 May a marked change had occurred in the structure of the adult mysid community (Fig. 6). In the two preceding months the relative size distributions of adult males and females had been similar, with very few fully adult females not actively breeding; these were all small and presumed to have matured recently. In May, out of 20 fully adult females present none were carrying broods. In contrast to the consistent size ranges of sub-adult and adult specimens over the summer period, the sizes of adult females had now started to increase slightly. The range of lengths of sub-adult males and females increased noticeably, principally by extension of the upper limit, due to growth. There was little recruitment of young suggesting breeding activity may have terminated some time previous to the collection of these samples. Some recruitment of sub-adult individuals (of unknown sex) from the larger neuter individuals probably occurred as the frequencies of the neuter size groups show progressive reduction within the larger size classes.

In June the trends apparent in May continued (Fig. 6). Neither reproductive activity nor juvenile recruitment were seen. The tendency towards increase in the length of the adult females and length ranges of sub-adult groups progressed further. An apparent decrease in the relative numbers of the adult males, first evident in May, had progressed further in June. The largest females and males had increased in length

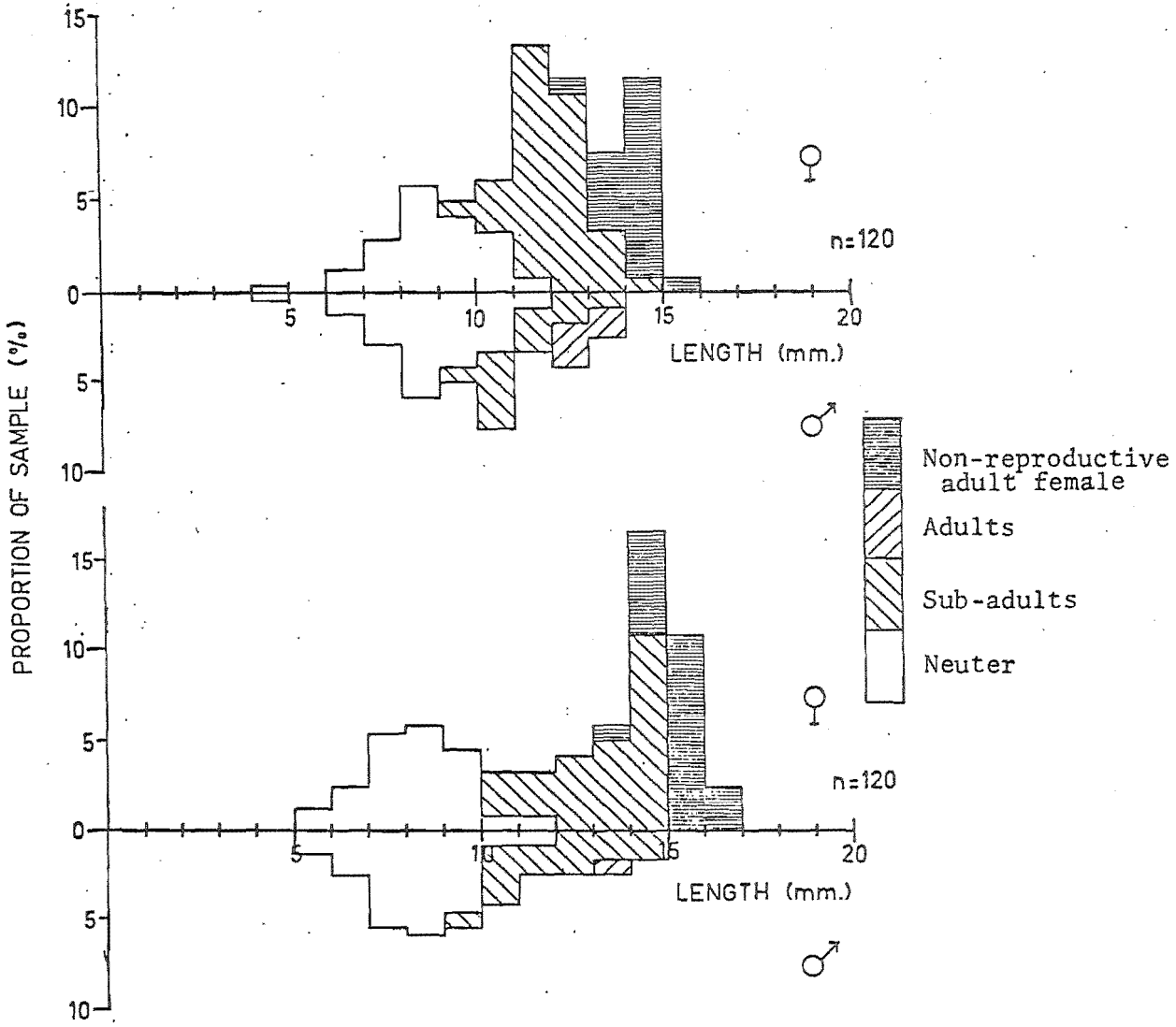

Fig. 6 Population structures sampled 6 May 1980 (top) and 9 June 1980 (bottom). Neuter specimens are plotted symmetrically about the X axis, females above the X axis, males below the X axis.

by 2.0 and 2.5 mm, respectively, since the last actively breeding animals were taken in March. Little recruitment to the adult female group was evident.

In the sample taken on 7 July the growth trends noted in June had continued resulting in a population having a dispersed length-frequency structure with a range in total length of 5.0 to 17.0 mm (Fig. 7). By the time of collection of these samples maturation into non-reproductive adult females had recommenced. There was no evidence of recruitment of adult males or active breeding. These samples were the last full series of samples collected during the study. At this time the lake water was at the lowest average temperature recorded during this study (7.9°C). The mean lengths and range in lengths of each group were:- Neuter 7.3 mm (Range 5.0 - 10.5 mm); Sub-adult Female, Mean 11.7 mm (Range 10.0 - 15.5 mm); Adult Female, Mean 15.3 (Range 13.0 - 17.0mm); Sub-adult Male, Mean 11.4 mm (Range 8.5 - 13.5 mm) and Adult Male, Mean 14.2 mm (Range 14.0 - 14.5 mm). These ranges in length differ markedly from those calculated for February samples. The overall male:female ratio was 0.40.

As a consequence of low mysid densities at individual sites and low mean mysid densities within the lake, the last two samples, taken in late winter and early spring, were substantially smaller than previous samples (N = 65 and N = 58 respectively). They therefore show greater sampling error. Allowing for the effects of random error the population sampled on 12 August appeared to have substantially the same structure as in July except for three differences (Fig. 7): individuals had matured to sub-adults and adults of both sexes at a shorter length; a significant mature male group had developed; and a single brood-bearing female was found, the first actively reproducing female collected since March when the mean water temperature was 12.1°C. The temperature at the collection site of the reproductive female in August was 9.0°C, the highest water temperature recorded during this period. Overall male: female ratio had increased further to 0.74.

Poor weather conditions and associated low mysid densities in littoral environments prevented the collection of the next sample series until 2 October 1980. Mean water temperature had then increased to 16.9°C. The sample contained numerous breeding females and four non-reproductive females at the lower end of the adult female length spectrum. Recently released juveniles were present in the sample from Station 2, although not in the sample selected for analysis. An incomplete

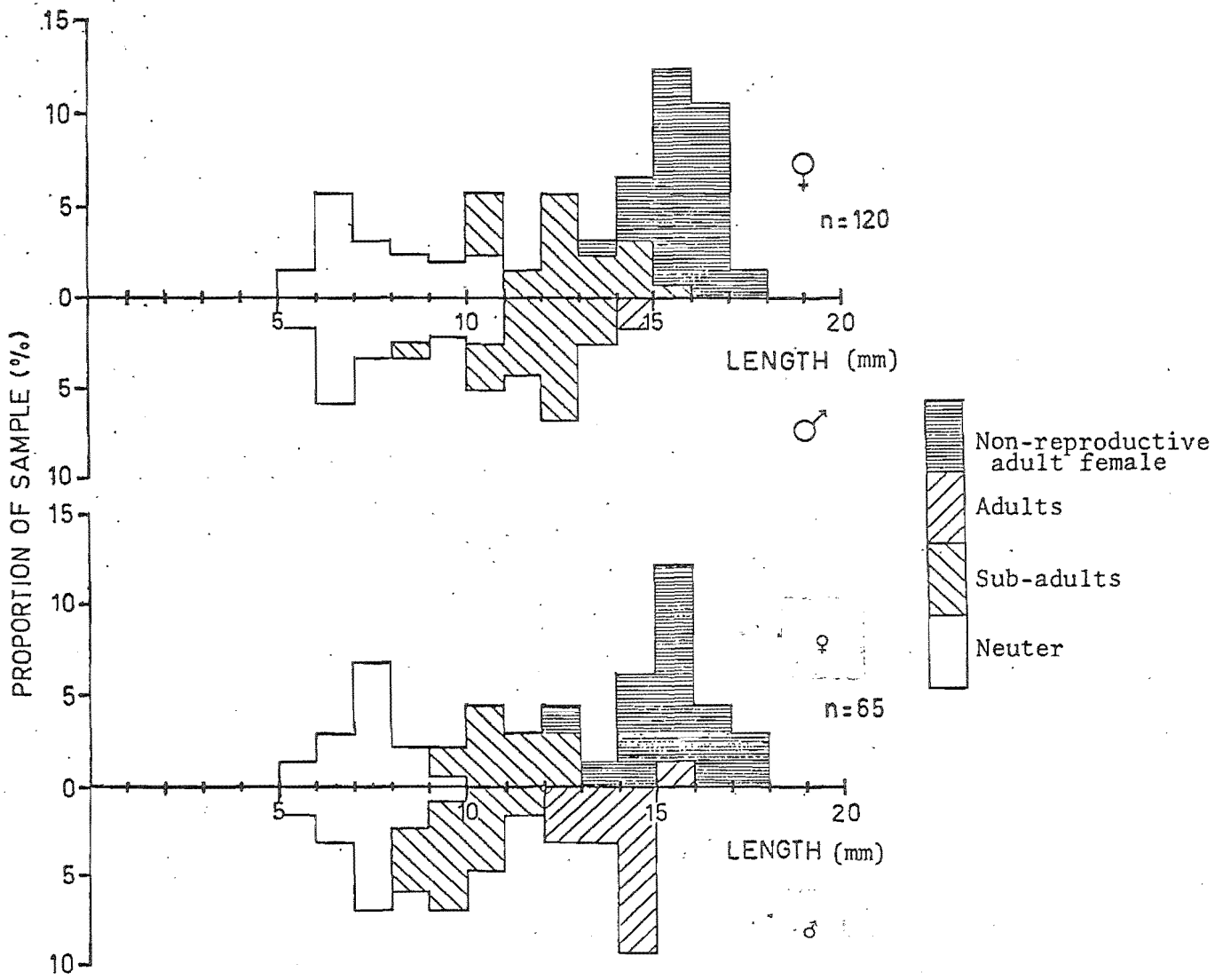

Fig. 7 Population structures sampled 7 July 1980 (top) and 12 August 1980 (bottom). Neuter specimens are plotted symmetrically about the X axis, females above the X axis, males below the X axis..

collection on 25 September contained several adult females of reproductive status (water temperature = 13°C). The smallest neuter components of the August sample had apparently grown 3.5 mm since August by 2 October (Fig. 8). A general growth and development of the neuter group into sub-adults and possibly adults was also evident. There was little evidence of the continued existence of the moderate numbers of 13 and 14 mm adult males present in August. The overall sex ratio was still at a high level (0.73). The population density at this time had reached the minimum recorded during this study.

3.3 DISCUSSION

The *Tenagomysis chiltoni* population investigated showed marked seasonal variation in density and structure. The extent to which this variation reflects changes in the population of the lake as a whole will depend on the efficiency of the sampling technique. Practical limitations restricted access to many habitats within the lake and necessitated use of a hand net (as used by Borghouts, 1978). Juveniles of various species of mysids may disperse (Mauchline, 1970a) to avoid wave action (Mauchline, 1971a) or may aggregate at different depths to adults of the same species (Clutter, 1969) sometimes resulting in the formation of a midwater peak of juvenile abundance (Siegfried, Kopache and Knight, 1979). Deepwater adult aggregations have been recorded for *Mysis stenolepis* (Amaratunga and Corey, 1975). Proximity of the surf zone (Clutter and Theilacker, 1971), surf-related distributions (Clutter, 1969) and avoidance of wave effects are recorded (Borodich and Havlena, 1973; Mauchline, 1971a). Variation in depth distribution (Beeton, 1960; Robertson, Powers and Anderson, 1968), substrate preference (Mauchline, 1971c) and relationship of mysid density to salinity (Heubach, 1969; Siegfried *et al.*, 1979) have been observed. Environmental influences upon sampled population density and structure are therefore well documented.

During this study attempts were made to minimise adverse effects of environmental influences on sampling efficiency. Surf zone and wave effects were avoided as much as possible by sampling in fine weather. Samples were taken to a maximum depth of 1.5 m. Lake Ellesmere has a mean depth of 2.1 m below m.s.l. (Hughes *et al.*, 1974) and lake level was about 0.8 m above m.s.l. during much of this study. Thus over half the mean depth of the lake was sampled. No mysid stratification was found in the lake but movement into deeper water was observed when wave height

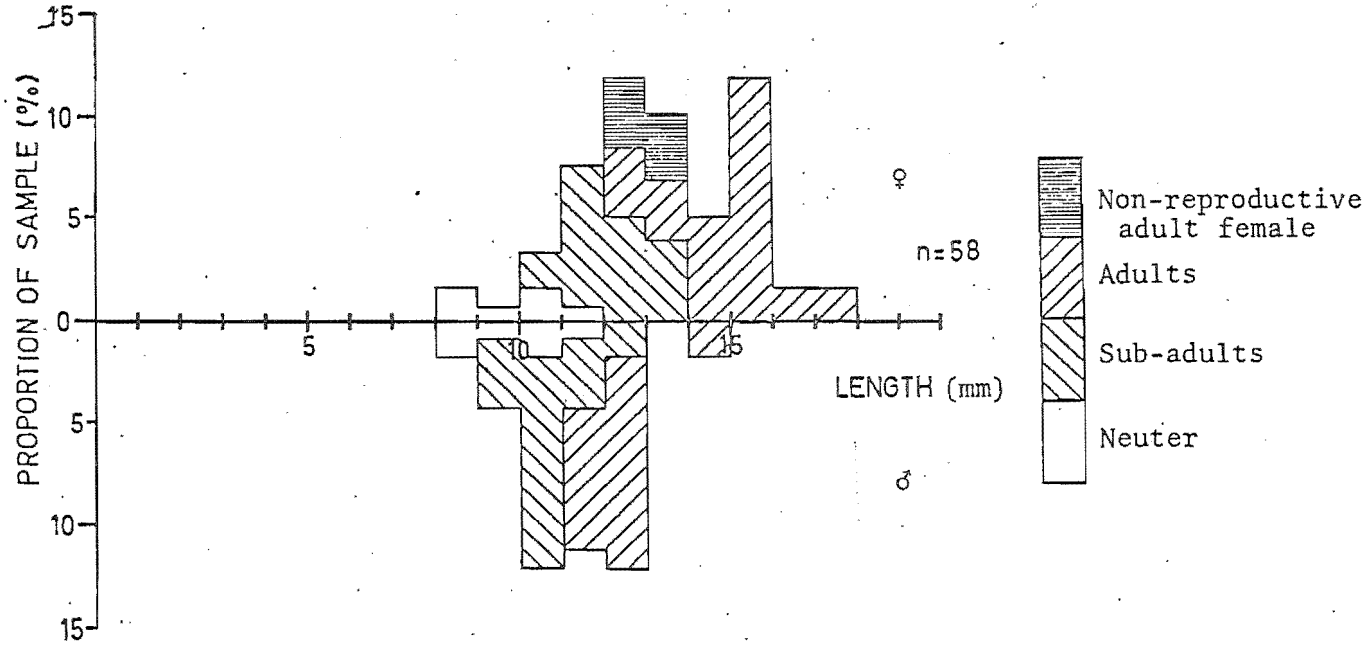

Fig. 8 Population structures sampled 2 October 1980. Neuter specimens are plotted symmetrically about the X axis, females above the X axis, males below the X axis.

exceeded 0.45 m. Mysid access to deeper regions than those sampled was possible but limited by very low inclination of the bottom beyond the littoral zone. All substrates from pebbles to fine silt on the Wentworth scale were examined to overcome substrate preference within the regions studied. Salinities recorded near the region studied (mean salinity 8.2‰ ± 0.97 standard error) were close to the mean salinity of 8.5‰ (± 0.41 standard error) within the lake as a whole (Mr I. Lineham, pers. comm.). As the study has excluded or minimised most of the disadvantages inherent in hand net sampling of mysid populations, the results are reasonably representative of the population of *Tenagomysis chiltoni* present in this region of the lake. The consistency of trends shown in mean mysid density estimates, population structure and sex ratios provide good evidence in support of this conclusion. Mr P. Kirk (pers. comm.) states that observations on the population dynamics of *T. chiltoni* in Lake Ellesmere seem to correlate very well with his observations on populations of *T. chiltoni* in the Waikato region of New Zealand.

The marked variation in mean mysid population density is of great interest to the ecology of the lake in view of the very high mysid densities recorded at times. The density recorded is probably an underestimate as the mysids were found close to the bottom during daylight hours, as has been observed with many other mysid species (e.g., Grossnickle and Morgan, 1979; Mauchline, 1980; Tattersall and Tattersall, 1951). Net avoidance is also common with mysids (Clutter, 1969) limiting sampling efficiency. The marked increase in population density between early November and late January coincides with the spring increase in water temperature and a phytoplankton bloom (Mr I. Lineham, pers. comm.) as was found also in *Neomysis mercedis* (Siegfried *et al.*, 1979). The phytoplankton bloom is unlikely to be a causative factor as planktonic algae were only ingested by *T. chiltoni* of some size groups in minimal quantities, but phytoplankton growth is possibly correlated with the growth and availability of filamentous algae and other plants which are eaten as the supply of both will probably be limited by available sunlight. The increase in population numbers is a consequence of an increased rate of maturation and the onset of reproductive activity within the overwintering population and their progeny. The marked decline of the population, first recorded in February and which continued until early May, is at a period of abnormally high lake salinity recorded locally in February, March and May 1980 (Fig. 2). This period

covers the time of release of spring and summer generation broods and the population decline was therefore unexpected. As stomach fullness indices reached maximum levels at all four sites over this period, and stomach contents during this period included the more nutritious dietary items in similar quantities to the period of maximal population growth, the population apparently was not subject to nutritional constraint, which could otherwise have affected population development (Morgan, 1980). The mysid *Praunus flexuosus* died rapidly when exposed to high temperatures (McLusky and Heard, 1971). *Mysis* species have a limited tolerance of low dissolved oxygen levels (Ackefors, 1969; Holmquist, 1959) but there is no evidence to suggest that dissolved oxygen concentration functions as a primary factor controlling their behaviour (Mauchline, 1980). During the period when salinity exceeded 7‰, water temperature and dissolved oxygen concentration showed no significant difference from the preceding periods during which rapid increase in population numbers occurred. Thermal, respiratory or nutritional constraints capable of producing the observed population decline are therefore improbable. The period during which salinities exceeded 7‰ showed close coincidence with the period of the decrease in population growth, which itself contradicted expectations based on observed population breeding cycles. It is therefore suggested that adverse salinity effects caused the observed decline in population numbers. Chlorinity limited the distribution and abundance of *Neomysis awatschensis* (Heubach, 1969). *Neomysis mercedis* had an observed distributional range of 1 - 30‰ salinity but was most abundant between 1‰ and 6‰ (Siegfried *et al.*, 1979). *Tenagomysis* sp. (probably *T. macropsis*) has a limited salinity tolerance (Greenwood and Jones, pers. comm.). Salinity can therefore influence the distribution of one species within the genus and further investigation is warranted with respect to *T. chiltoni*. Salinity can influence population density by habitat displacement and compression (Siegfried *et al.*, 1979). As no population recovery was observed after the salinity again fell below 7‰ and recolonisation from regions which had maintained lower salinity levels became possible, the effect of abnormally high salinities suggested was probably widespread. Abnormally high salinity was recorded over much of the lake area during this period by Mr I. Lineham (pers. comm.). As the period of adverse salinity extended over most of the reproductive periods of the first and second cohorts (Figs 2, 4, 5 and 6), salinity stress may have operated on larval stages which are more vulnerable to salinity change than the adult stages (Vasblom and Elgershuizen, 1977 cited in Mauchline, 1980).

Shortly after the lake returned to within its normal salinity range active reproduction ceased until the end of winter (Fig. 6) preventing recuperation of the population. Due to natural mortality, the population continued to decline slowly over the winter to a minimum in early October 1980. Shortly afterwards, *T. chiltoni* density increased as a result of reproduction by the overwintered population. This overwintered population may be formed from more than one cohort.

There was apparently no active breeding over the winter months preceding this study as the first sample taken (26 September 1979) showed evidence of brood formation without any small mysids being present to indicate that release of the spring generation had begun. Lack of breeding during winter months has been recorded frequently in the literature (Borghouts, 1978; Borodich and Havlena, 1973; Mauchline, 1980), and is probably indicative of severe climatic conditions (Mauchline, 1980).

By 8 November the bulk of the population consisted of sexually undifferentiated spring generation individuals which had completed their larval development and been released since the last collection date. The adult members of the overwintering generation, which had produced the spring generation, were dying but those remaining were still actively reproducing. Mature females die one to two weeks after final brood ejection occurs in *Mysis stenolepis* (Modlin, 1979) possibly resulting in very few females with an emerged brood being present in some populations (e.g., Mauchline, 1967). Male *Mysis stenolepis* die soon after sperm transfer (Amaratunga and Corey, 1975), and all overwintering animals die during the two months succeeding spring generation release in *Neomysis integer* (Mauchline, 1971b) or by mid-summer in *Paramysis arenosa* (Mauchline, 1971a). There was no evidence supporting mortality due to ageing of *Metamysis elongata* (Clutter and Theilacker, 1971), but such mortality is present in many other species (Mauchline, 1980). In *Tenagomysis chiltoni* the survivors of the overwintering generation and the spring generation showed rapid growth after September, associated with maturation and a higher selective mortality of males in overwintered mysids. Mature male deaths have been recorded one month before mature female deaths in *Mysis relicta* by Hakala (1978), and in *Mysis stenolepis* by Amaratunga and Corey (1975) and Modlin (1979).

By mid-December a significant proportion of spring generation individuals exhibited secondary sexual differentiation and 17% were fully

adult. Most of the overwintered generation were now dead. The low recruitment of juveniles, and small proportion of spring generation adult females actively breeding (6%), suggests that the spring cohort had not yet produced significant numbers of the summer generation. The low recruitment levels observed are principally attributable to the breeding of the remaining overwintered individuals. The pronounced population increase observed since November is due to an earlier period of reproductive activity by the overwintering generation.

In January small numbers of adult females were present but juvenile recruitment was evident, suggesting that females may breed rapidly and die soon after maturation. However the low sample number (N = 90) and inconsistency with results from adjacent sampling periods indicates that the unusual result is most probably attributable to sampling error. The growing summer generation cannot be easily separated from the spring generation in this or subsequent sampling periods, but must be present as the overwintering generation is now absent. The post-larval mysids present must therefore be summer generation progeny of the spring generation. Some of these post-larvae must have been released recently as the smallest individuals had lengths only marginally greater than those of eyed larvae. Populations of mixed age with obscured generations are common in Type E mysids (Mauchline, 1980). Salinities in the lake were at normal levels and the population showed a great increase in numbers and juvenile recruitment, typical of other Type E mysids studied during this season (Mauchline, 1967, 1971b, 1971d).

During mid-January mean lake chlorinity was over twice the normal modal level (Mr I. Lineham, pers. comm.) but saline influx was not shown in the littoral salinity samples until February, presumably due to considerable freshwater influx from Harts Creek. This suggestion is supported by low salinities recorded at Sites M and 1. Analysis of the rate of increase from mean density determinations showed that the rate of population increase, while still positive, had decreased markedly compared with the November - December value. It is probable that populations elsewhere in the lake were already adversely affected by high salinity, but that local populations were protected from adverse saline influence by the presence of a zone of low salinity of limited lateral extent.

By 19 February the population showed negative growth in numbers associated with minimal juvenile recruitment in spite of the presence

of numerous brood-carrying females. Post-larval individuals had undergone growth and maturation since January, but without replacement of young individuals by the growth of successive brood releases of the spring generation. The larval stages are maintained in an environment partially osmotically regulated by the parent (McLusky and Heard, 1971), and exhibit a more restricted salinity tolerance range than the parental female with a salinity dependent developmental rate (Vlasblom and Elgershuizen, 1977 cited in Mauchline, 1980). Exposure of post-larvae to high salinities upon brood release could provide immediate and extended osmoregulatory problems to a greater degree than those experienced by older juveniles and adults. A size-dependent mortality factor capable of producing the observed low recruitment of post-larvae in the presence of reproducing adult females is therefore feasible. This factor possibly reduced post-larval recruitment of *T. chiltoni*. That the effect is at most only partial is demonstrated by the continuing recruitment, at a low level, and evidence of less growth within the shorter mysid length groups in succeeding months than would be expected if no post-larval recruitment had taken place.

During March a similar length-frequency distribution was found. Slow recruitment of post-larvae in the presence of abundant actively-reproducing females was apparent with a slight population increase. Salinity was now close to normal levels recorded during this study and successful breeding was occurring at a low level. The few non-reproductive adult females present were shorter than most reproductive adult females and are assumed to be newly developed adults in which brood extrusion into the marsupium had not yet occurred.

The next series of samples, collected on 6 May, showed a complete absence of developing embryos between fully developed oostegites. This lack of embryonic development and associated post-larval additions to the population characterised all samples taken until August, when a single reproducing female was found. Initially fully adult marsupia, characteristic of females which have produced a brood, were observed; later in the winter period post-reproductive oostegite structures were not observed in adult females. It is assumed that the loss of recognisable post-reproductive females from the population resulted either from the gradual mortality or a structural moult modification of post-reproductive females. The preceding decreased male:female ratios suggest that sexually selective male mortality was occurring. Where cohorts were separable it was observed that this male mortality was followed by female mortality in the succeeding two months.

During the winter, development of the population in terms of both growth and maturation was slow. Fully adult individuals showed a gradual increase in length throughout the winter. As, on ceasing to breed, growth of the largest adults recommenced, nutritional factors do not seem to have limited the breeding season, but rather energy put into reproduction over summer was re-allocated to continue interrupted adult growth. This period of further growth is shown by the observed differences in length between breeding adults of the overwintered generation, and of the spring and summer cohorts. Different cohorts produced adult females of different sizes. This influences the reproductive potential of the species since a correlation was found between total length and brood size in *T. chiltoni*, and in many other species (e.g., Clutter and Theilacker, 1971; Morgan, 1980; Mauchline, 1980).

A few members of the overwintering population ended their sexually inactive phase prior to 12 August when a single adult female carrying a brood was captured. By 25 September nearly all adult females were actively reproducing. The majority of the population extruded their first brood of the season between mid-August and mid-September 1980, at a similar period and at similar sizes to the start of the 1979/80 breeding season. The recommencement of embryonic extrusion coincided with the initial rise in water temperature associated with the increased incident radiation in late winter (Fig. 2). Cushing (1959) suggests a link between onset of reproduction and dietary thresholds, while Siegfried *et al.* (1979) record that spring increase of *Neomysis mercedis* was associated with increased temperature and a phytoplankton bloom. This statement applies to the maximum increase in the density of *T. chiltoni* in the spring, but the overwintered population bred two months before the peak of the phytoplankton or filamentous algae bloom and prior to significant improvements in the quality and quantity of their diet. This suggests that temperature or its associated variables induced breeding activity. Water temperature can affect reproductive activity either through effects on brood development time (Jepsen, 1965), by acting as a primary factor regulating larval rate of development in all mysid species (Morgan, 1980) or by influencing generation time (Lasenby and Longford, 1972). Omori (1971) states that larvae of the penaeid shrimp *Sergestes lucens* exhibited decreased growth and developmental rate with decreasing environmental temperature, and that larvae ceased feeding when temperature decreased from 10°C to 6°C. In view of the strong influence of temperature on the reproductive physiology of mysids and other animals and

the decreased quality and quantity of food resources during this period, thermal induction of brood extrusion into the marsupium seems probable. As has been found in other mysid species (Mauchline, 1980), winter breeding may be absent in these regions of more severe climatic conditions than are present in the rest of the distributional range of *T. chiltoni*.

With the growth and development of the neuter individuals towards maturity and the return of the adult females to reproductive status, by October 1980 a complete annual cycle had been followed. The sampling programme had shown the release of at least two broods over the period of spring and summer. The summer generation had taken two months to develop from post-larvae to breeding adults. As similar temperatures prevailed over the next two months, preceding the onset of winter reproductive inactivity three to four months later, sufficient time (at the prevailing temperatures) existed for the release of a third cohort by the summer generation. No direct evidence was found for the release of such a brood.

Mauchline (1980) states that individual cohorts of species producing three or more generations per year are difficult to identify in natural populations as generations often overlap. This study was designed primarily as a feeding study and the period between samples is therefore quite long for sequential length-frequency analysis to identify a possible third cohort. Therefore indirect evidence of a third, "Autumn", generation was examined.

Changes in the sex ratio within a population could result from differential mortality of males and females. This ratio varies between samples and between seasons but no consistent reason for these fluctuations is apparent in mysids (Mauchline, 1980). Some lake-dwelling species of mysids show a degree of isolation from surrounding populations (Morgan, 1980). In Lake Ellesmere the strategy employed to lower the lake level results in the lake being isolated from marine mysid populations for protracted periods. No temporary immigrant mysid species have been recorded within the lake, and the inflowing rivers support only *T. chiltoni*. For the purposes of this study of the population dynamics of *T. chiltoni* the population is effectively isolated, and consequently devoid of perturbation by influx of components of other *T. chiltoni* populations of differing development. Mauchline (1980) does not quote any sex ratio analysis which examines sex ratio fluctuations for individual cohorts

against time. In this study the unusual nature of the habitat examined, and the method of analysis employed, disclosed an interesting cyclic phenomena which correlates well with seasonal length-frequency variations. For both the distinct cohort breeding periods up to February 1980 for the population breeding in the spring of 1980, the adult male:female ratio was highest at the times when large numbers of adult females carried broods (Fig. 9). No full samples were collected after October 1980 so what happened to the adult male:female ratio after this is not known; however, after the earlier breeding periods of overwintered and spring cohort individuals, males showed a marked decline relative to the females in the population. After January 1980 spring and summer generations are not distinguishable from population length-frequency histograms, and hence cannot be separated into cohorts for analysis. In March 1980 the post-breeding decline of the adult male:female ratio is reversed by a small, but noticeable, increase in the relative number of males present. This increase occurs during the period when it is proposed that an autumn brood may be released and coincides with a small increase in post-larval recruitment within the population. A smaller increase in overall male:female ratio is evident one month earlier. It is therefore thought to represent the increase in the proportion of summer generation males associated with production of an autumn generation which has been reduced in apparent extent by a continuing decline in the post-reproductive adult male:female ratio within the spring generation; this was due to an inability to separate spring and summer generations at this time. A subsequent post-reproductive decline is associated with the peak in adult male:female ratio. The adult male: female ratio reaches a minima coincident with the non-reproductive phase of the adult females during winter, and subsequently increases as overwintered adults develop physiologically before the spring breeding period. The overall sex ratio shows the same changes, but usually about one month earlier than the adult sex ratio trends, which reflects changes in the sub-adult population associated with the population cyclicity. In the spring and summer generations adult male specimens show a shorter length range than adult females, a population feature which may be associated with a shorter adult life or the allocation of energy reserves, surplus to the organism's immediate requirements, to reproductive activities. Low sex ratios cannot be due only to differential seasonal recruitment rates for males and females unless complex and unusual fluctuations occur. The literature provides some observations and partial

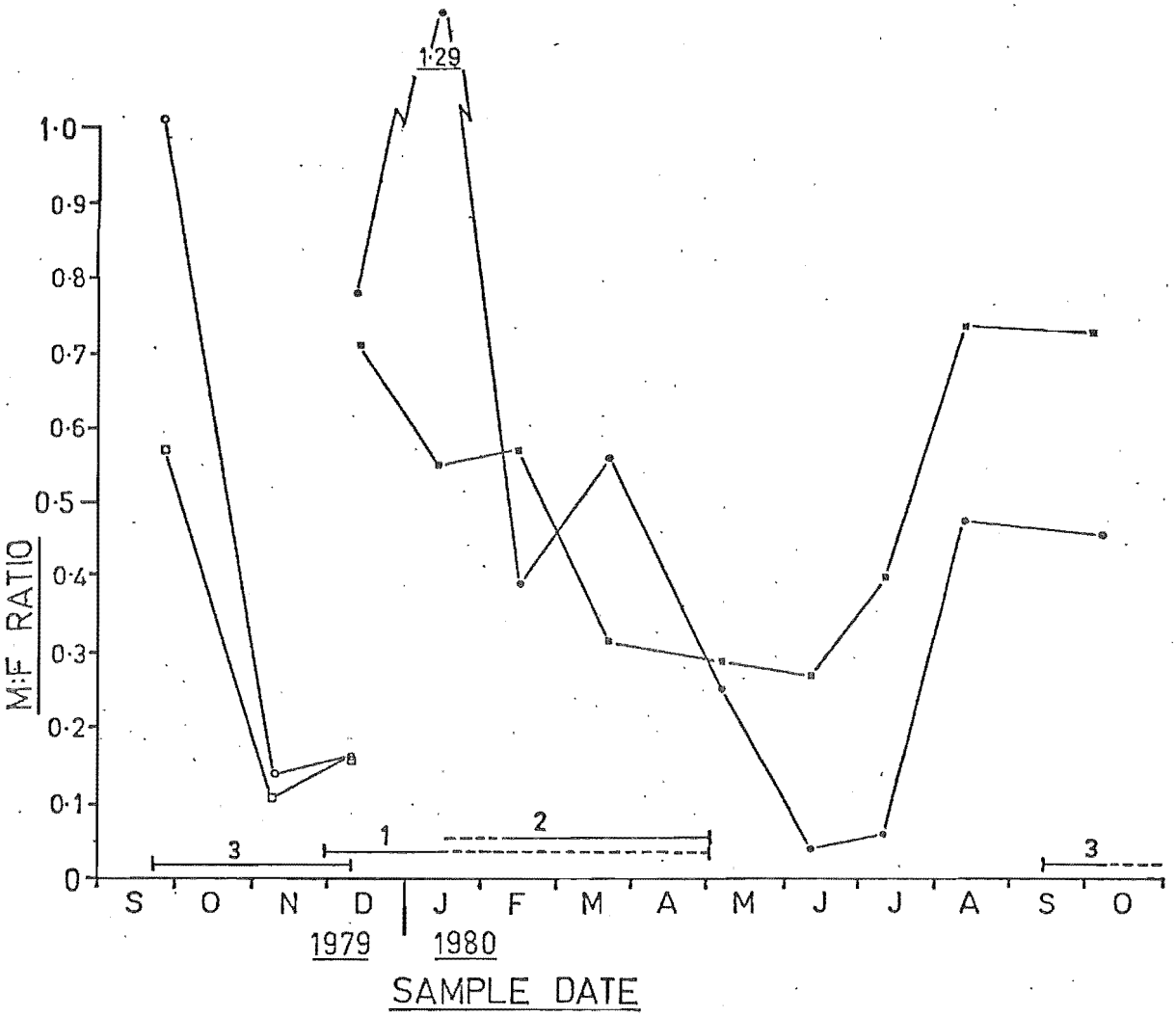

Fig. 9 Seasonal variation in adult male : female ratio and overall male : female ratio. Circles = adult male : female ratio, squares = overall male : female ratio (hollow = 1978/79 overwintered mysids, solid = all subsequent cohorts). 1 = spring generation breeding period, 2 = summer generation breeding period, 3 = overwintered mysids breeding periods.

explanation of the suggested earlier death of adult males compared with adult females. In some studies of mysids, the male:female ratio has shown mortality-associated reduction due to the death of males before the female population of similar length (e.g., *Mysis relicta*, Hakala, 1978; *Mysis stenolepis*, Modlin, 1979), which is capable of producing Mauchline's (1967) observation of sexual inequality in some environments. The number of broods produced by females of different species is variable, and that the female may produce only a single brood (Mauchline, 1980). Modlin (1979) observed laboratory fatality of adult females 1 - 2 weeks after brood ejection. *Tenagomysis chiltoni* probably produces more than a single brood as numerous well developed eggs are frequently present in the ovaries of brood-bearing females. Brood time is variable and related to environmental temperature (Blegvad, 1922; Mauchline, 1980; Morgan, 1980) and salinity (Vlasblom and Elgershuizen, 1977 cited in Mauchline, 1980) but is 12 - 25 days for various mysid species at the environmental temperatures encountered during the active breeding period of *T. chiltoni* in Lake Ellesmere (data from Mauchline, 1980). The female therefore has a probable minimum adult survival period of 24 - 50 days, assuming that at least two broods are normally produced by an adult female. Hakala (1979) demonstrated an almost total loss of organic carbon reserves by adult male *Mysis relicta* while actively breeding, suggesting that energy depletion is a possible causative factor in sexually selective mortality. While the female must survive to release at least one brood to breed successfully, in a short breeding season it may be a more stable evolutionary to allocate all available time and energy to a short burst of sexual activity rather than allocating potential breeding time for the location and collection of food, and thereby ensuring a longer breeding period during most of which uninseminated adult females would be scarce or absent.

Adult males ingested an average of 52% of the volume of food ingested by adult females; this figure is probably an overestimate of ingestion by males while breeding as sexually inactive males, which are presumably feeding normally, are included in the calculation. In a variable food resource it is not possible however to tell whether the males fed less actively or the females fed more intensely. Some of this difference in ingested volume may be size-related rather than sex-associated.

The level of the pre-breeding peak in both the overall and adult male:female ratio is possibly influenced by protandry, as observed in

many insect species (Wiklund and Fagerström, 1977), however, the later development of females is unlikely, as an isolated effect, to produce changes in male:female ratios of the magnitude observed.

Irrespective of the cause of the observed phenomena, indirect evidence for the production of a third cohort is provided by sex ratio changes associated with the predicted breeding period of the second cohort and the marginal increase in post-larval recruitment in March 1980. The author therefore believes *T. chiltoni* is producing at least three generations within an annual cycle and hence belongs within Type E of Mauchline (1980). The overwintering generation is probably composed of autumn generation mysids together with some remaining summer generation individuals.

Fluctuation in the density of the mysid population of the degree observed can be expected to affect the intensity of resource utilisation per unit area, ultimately influencing food resource levels. Threlkeld *et al.* (1980) have demonstrated a density-dependent influence of *Mysis relicta* upon zooplankton diversity and abundance. As availability exerts an influence upon predator choice of prey (Murdoch, Avery and Smyth, 1975), mysid population density may affect the composition of populations both of preferred prey species and of competing species, ultimately influencing the mysids' own ingestion through changes in preference (Newsome and Gee, 1978) and prey size structure (Bevan, Winner and Wallen, 1978) resulting from changes in prey communities due to the predation (Neill, 1975; Threlkeld *et al.*, 1980).

In addition to changes in the total numbers of the mysid population, significant changes in the size and sexual structure occurred which have caused dietary changes through their influence upon predatory ability of other mysids (Cannon and Manton, 1927; Kost and Knight, 1975; Siegfried and Kopache, 1980; Sitts and Knight, 1979) and nutritional requirements of other animals (Carefoot, 1973; Dabrowski, 1979; Dethier, 1967, 1970; Emlen, 1966, 1968; Harper, 1967; Pulliam, 1975). In this study, considerable variation in the composition of the population occurred within and between the different cohorts produced by *Tenagomysis chiltoni* both between different sites at the same time, and between different sampling periods.

CHAPTER 4

INGESTION BY *TENAGOMYSIS CHILTONI* IN RELATION TO SOME INTRINSIC FACTORS

4.1 INTRODUCTION

Feeding strategies result from the complex interaction of physiological and environmental variables. The optimal strategy may never be attained in practice as it will be limited by the ability of an animal to detect changes in its internal and external conditions (Pyke *et al.*, 1977; Vahl, 1979) and to modify its feeding behaviour on the basis of this sensory input to increase the overall nutritional benefit derived from its diet. The influence of developmental and physiological parameters on general and specific hungers, and the probability of successful encounter with a prey organism, may be marked. An understanding of the feeding apparatus and condition of an organism is therefore essential to the interpretation of food resource utilisation by the organism.

The functional morphology of feeding appendages has been studied in several species of mysids (see Cannon and Manton, 1927; Gelderd, 1909; Mauchline, 1980; Tattersall and Tattersall, 1951). Feeding mechanisms of the unspecialised mysid *Hemimysis lamornae* were investigated in the classic study of Cannon and Manton (1927) which corrected some misinterpretations of previous studies. Cannon and Manton defined two principal feeding methods, filtration on the maxillules and raptatory feeding using the endopods. Factors influencing choice of feeding method have not been investigated comprehensively for any member of the Order Mysidacea.

The influences of developmental changes on diet have been investigated for a single species, *Neomysis mercedis*, by Kost and Knight (1975) and Siegfried and Kopache (1980). They showed marked differences in the diets of mysids of different lengths, but differed in their opinions of the value of the relative contributions of different dietary components in almost identical geographic locations. Edmondson and Murtaugh (1980) also showed a clear relationship between mysid size and maximum prey (*Daphnia thorata*) size. A few studies have shown the influence of sexual development upon ingestion in members of other orders of (Glasser, 1978; Lat, 1967; Menge, 1972; Nybakken and Eastman, 1977), but none in the Order Mysidacea. Carefoot (1973) suggested that preference of the isopod *Ligia pallasii* may have been determined by availability. During this study, no studies were

found on the influence of hunger on the ingestion of crustaceans. Estabrook and Dunham (1976) conclude that well fed predators may specialise more; satiation may be a determinant of selection of diet by an organism (Emlen, 1966).

In this study an attempt was made to determine the degree of influence exerted by total length, sexual development and hunger (as inferred from fullness indices) on the nature of the food ingested by *Tenagomysis chiltoni*. This work was done with the intention of developing an understanding of the effects individual and cyclic population changes may bring about in the ingestion of *T. chiltoni*. This knowledge is a prerequisite to developing an understanding of the observed food resource utilisation by *Tenagomysis chiltoni*.

4.2.1 Errors in the Determination of Dietary Composition

Numerous sources of error recorded in determining the diet of an organism (e.g., Berg, 1979; Houston, 1973; Moore, 1977; Windell, 1978), many of which could operate in the study of the feeding habits of members of the Mysidacea. In the present study the experimental technique was designed to exclude avoidable known sources of error.

During the capture of an animal both normal foods and foods not normally available may be concentrated artificially within a net; this may result in ingestion of prey within the net, as suggested by Sitts and Knight (1979) while working on *Crangon franciscorum* and *Palaemon macrodactylus*. This source of error was minimised in this study by using short net hauls, taking less than 30 seconds to complete, and a mesh base to drain the end of the net when removed from the water, thus preventing further feeding by *Tenagomysis chiltoni*.

Pavlov (1971) suggested that *Euphausia superba* ingests principally the fluids and soft tissues of diatoms, rejecting many frustules in a '*bol alimentaire*' not formed by the Mysidacea (Cannon and Manton, 1927). This suggests that the identifiable hard parts in the stomach may not be fully representative of the tissues from which an organism derives sustenance. Conversely, Fisher and Goldie (1959), working on another euphausiid *Meganyctiphanes norvegica*, stated that only material within the digestive tract should be considered as food as material collected between the feeding appendages may have been collected while the organism was in the net. No rejection of diatom frustules, or other foods less than 1 mm in length, by adult *Tenagomysis chiltoni* was observed. Fisher and Goldie's (1959) view was therefore adopted, with the reservation of Cummins (1973)

that material present in the digestive tract is not necessarily of nutritive value to the consumer. Observations of *T. chiltoni* consuming corpses of their own species in aquaria suggested that the softer abdominal and thoracic regions were consumed first and that the consumer's appetite could be sated, causing rejection of the corpse, without ingestion of thoracic limbs or other hard parts used as indicator particles during counts. In a laboratory trial using 15 *Paracorophium lucasi* as a prey organism no rejection of the gnathopod and tarsal claws used as count indicator particles was observed during predation; the calculated volume of *P. lucasi* tissue ingested probably closely approximated the actual volume ingested by the mysid. No suitable chironomid larvae were available in the lake at that time to test *T. chiltoni* for rejection of count indicator particles used for *Chironomus zealandicus*. However, in view of the large volume of soft tissues present in even a small specimen of *C. zealandicus* compared with the space available within the digestive tract of an adult mysid, and the strength of the head capsule of *C. zealandicus*, rejection of these count indicator particles and the consequent underestimate of the nutritive value of chironomids to *T. chiltoni* is possible. *Chironomus zealandicus* did not make a major contribution to the diet of most of the subdivisions of the sampled populations of *T. chiltoni* employed in this investigation. Significant solid and fluid loss from a prey item may occur prior to the ingestion of *Daphnia* sp. or chironomid larvae (Prestige, 1979), thereby causing an overestimate of the food value of the prey item when using count indicator particles to calculate the volume of tissue ingested. The degree of inaccuracy, caused by tissue and fluid losses during the ingestion of prey, is not known in this study.

Moore (1977) showed that no regurgitation or defaecation occurred when live specimens of seven species of benthic herbivores were placed in normal concentrations of fixatives or preservatives, but cites examples when this did occur. Live *T. chiltoni* lost no detectable quantity of ingested material when placed in 4% formaldehyde solution, the fixative used at the time of collection.

Analysis of foods present within different regions of the digestive tract may produce significantly different results (Berg, 1979; Pavlov, 1971) due to differences in the rate of passage of different dietary components within the various regions of the gut (Berg, 1979; Hill, 1976; Houston, 1973; Nadin-Hurley and Duncan, 1976), and is also suggested by the data of Nybakken and Eastman (1977). This is especially true in the

Order Mysidacea where the stomach filter retains food within the cardiac chamber of the stomach until mastication reduces the food particles to a sufficiently small size to allow passage through the filter (Gelderd, 1909). By the use of count indicator particles which were small, and readily detached from the main bulk of a food particle, but remained a stable unit during mastication this source of error was largely removed from the current study, except possibly in the cases of filamentous algae and chironomids. Nadin-Hurley and Duncan (1976) record the slow passage of filamentous algae down the digestive tract of Cladocera; in the Mysidacea a long thin strand may be resistant to mastication by the stomach armature and have difficulty passing over the stomach filter. The only viable count indicator particles for *Chironomus zealandicus* were the mandibles and the labial plate. The labial plate moved through the stomach at a significantly slower rate than a mandible ($\chi^2 = 17.36$, df = 1, $p < 0.001$, n = 21), probably due to its retention on the large head capsule and therefore was rejected as a count indicator particle. The mandible moved through the stomach filter much more rapidly, but appeared to remain attached to the head capsule for a while; this would increase the calculated volume of chironomid tissue in the diet relative to the actual volume consumed, and would tend to offset calculation errors produced by head capsule rejection.

The volume of tissue attributed to a given count indicator particle was constant, with the exception of count indicator particles for the largest prey organisms (*Paracorophium lucasi* and *Chironomus zealandicus*) which were less numerous in mysid stomachs, allowing measurement of each count indicator particle and use of a regression equation to calculate tissue volumes. This procedure introduced an error in calculated tissue volumes due to size variation within each prey species, and in the case of copepodites (which were rarely ingested) as a result of the reduced number of count indicator particles on smaller copepodites, which partially offsets errors due to the reduced volume of the smaller copepodites. These errors were not avoidable without an unacceptable increase in the workload. As only stable count indicator particles were used in this study, Hansson's (1970) criticism (cited in Houston, 1973) that conversion factors used in the analysis of diet may be erroneous due to different fragmentation rates in different seasons, is not applicable, except possibly in the case of macrophyte detritus where limited variation in the observed height of fragments examined under the microscope occurred during the study. Naked forms [i.e., without hard

parts] may not be recognisable within the gut (Marshall and Orr, 1962). Some chlorophytes may have been ruptured during mastication and thus lost their turgidity, and consequently their recognisable characteristics. These forms appeared to be of minimal importance in the diet of *Tenagomysis chiltoni*.

As the stomach contents of *T. chiltoni* were stored at low temperature (≃3°C) and prepared for microscopical examination within a few days of the specimens being collected, errors due to differential digestion rates between different categories of food, recorded by Berg (1979), Moore (1977) and Pavlov (1971), should be small. The cardiac chamber of the stomach of *T. chiltoni* constitutes roughly 70% of the volume of the whole stomach. As this chamber does not contain digestive enzymes (Gelderd, 1909) the effects of differential digestion are likely to be small. An attempt was made to de-activate digestive enzymes by using a formaldehyde fixative, but the effectiveness of this measure is unknown.

4.2.2 Relationship of Fullness of Digestive Tract to Nature of Foods Ingested

As a predator seeks to maximise its energy intake (Doyle, 1979; Lam and Frost, 1976; Lehman, Self and Jumars, 1978), within constraints created by specific nutrient requirements (Pulliam, 1975), a hungry selectively-feeding animal may fill the reduced space available in the digestive tract with foods having a higher nutritional value than a sated animal (Emlen, 1966; Estabrook and Dunham, 1976). Since food preference has been demonstrated in some insects (Cianciara, 1980; Dethier, 1970), this dependence of diet upon an interaction of food quality and hunger was postulated as a test for the operation of food preference in *Tenagomysis chiltoni*. The degree of fullness of the stomach and intestine was used as an operational definition of hunger; stomach fullness controls appetite in fish (Vahl, 1979). Initially, the diet of *T. chiltoni* from all samples analysed was determined. To minimise seasonal effects the analysis was then restricted to the period between January and May. In these months mysids ingested a more nutritious diet. This analysis mathematically excluded *Chironomus zealandicus*, as ingestion of this species was very variable and possibly given an incorrectly weighted significance in the food volume calculations used. The richer diet consumed should, theoretically, have produced a more pronounced degree of preference.

The diet of *T. chiltoni* consisted mainly of diatoms, filamentous algae, macrophyte detritus and other plant tissue. Animal tissues formed a smaller proportion of the diet, and consisted of planktonic and benthic components.

When all individuals subjectively assessed as having a stomach index of 0 were analysed as a group the percentage composition of their diet was 4% diatoms, 35% filamentous algae, 56% macrophyte detritus and 5% animal tissues, principally *Gladioferens pectinatus* (Fig. 10).

Individuals having a stomach index of 1 had ingested a larger mean volume per individual, relative to individuals having a stomach index of 0, higher proportion of diatoms (12%), larger volumes but a similar proportion of filamentous algae (36%) and a reduced proportion of macrophyte detritus (43%). The total contribution of all animal dietary components increased to 9%, 5.5% of which was composed of *G. pectinatus* tissue.

Individuals having a stomach index of 2 had ingested a larger mean volume but similar proportions of diatoms (12%) and 1.3 times the volume, but a reduced proportion of filamentous algae (30%). Macrophyte detritus contributed 1.6 times the volume of food compared with stomach index 1 individuals, but had only increased marginally in proportional contribution (46%). Animal components of the diet of stomach index 2 individuals contributed over 11% of the calculated ingested volume, a small percentage increase but nearly three times the volume ingested per individual, similar proportions being contributed by *G. pectinatus* (4.5%) and *Chironomus zealandicus* (4%).

Individuals having a stomach index of 3 ingested similar quantities and proportions of diatoms (13%), filamentous algae (27%) and macrophyte detritus (50%) to stomach index 2 individuals. Animal tissues were present in similar proportions (10%), but were composed principally of *G. pectinatus* tissues (9%).

Individuals having a stomach index of 4, the maximum index value, ingested slightly more diatom tissue (14%) and a moderately reduced volume and proportion of filamentous algae (16%) and plant detritus (41%). The calculated mean ingested volume of animal tissue had increased to nearly four times the volume of that ingested by stomach index 3 individuals and contributed 28% of the diet. 20% of the calculated dietary volume was composed of *Chironomus zealandicus* tissues and only 5% by *Gladioferens pectinatus* tissues.

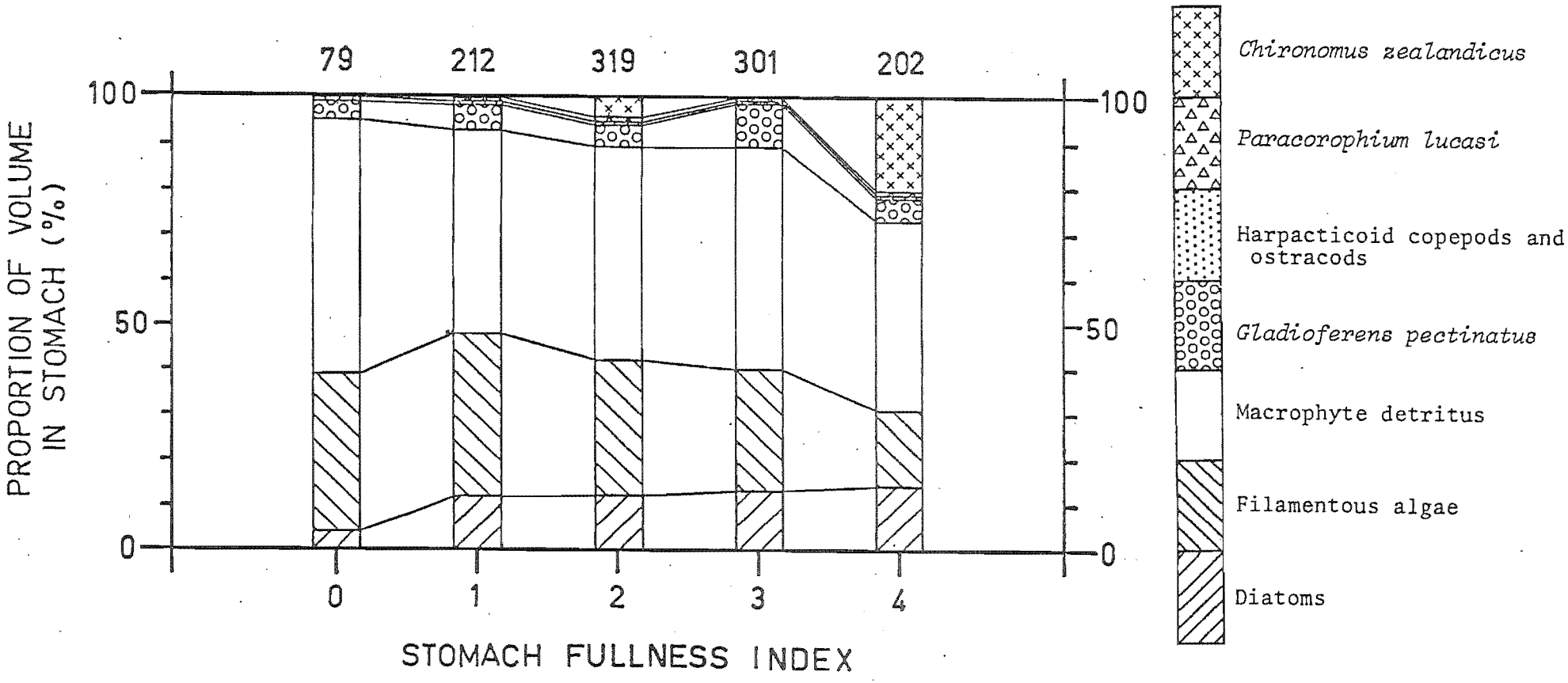

Fig. 10 Percentage composition of the diet as a function of the stomach fullness index over the annual cycle studied. The number of specimens of each group is given at the top of each bar graph.

The mean volume of food ingested by mysids from each stomach index class exhibited a linear relationship to the value of the stomach index. The mean volume of food present in the stomachs of individuals having stomach feeding indices of 0 to 4 was 0.008, 0.013, 0.021, 0.019 and 0.035 million cubic millimetres respectively, supporting the accuracy of the subjective stomach fullness index.

All mysids having an intestinal index of 0 had a combined diet composed of 12% diatoms, 24% filamentous algae, 45% macrophyte detritus and 19% animal tissues (8.7% *G. pectinatus*, 7.5% *C. zealandicus*) (Fig. 11).

Mysids having an intestinal index of 1 ingested slightly larger volumes but similar proportions of diatoms (13%) and macrophyte detritus (46%). Filamentous algae were ingested in larger quantities, compared with specimens having an intestinal index of 0, and comprised a greater proportion of the diet (31%). The volume of animal tissue ingested fell by a factor of 0.69 (compared with specimens having an intestinal index of 0) to 10% of the volume ingested, and was composed of *G. pectinatus* (7.7%), harpacticoid copepods and ostracods (0.4%), and *Paracorophium lucasi* (1.6%).

The stomachs of individuals having an intestinal index of 2 contained nearly twice the volume of diatoms, filamentous algae and macrophyte detritus in similar proportions (11%, 26% and 43% respectively) to the proportions of these foods ingested by specimens having an intestinal index of 1. The volume and percentages of all animal tissues ingested quadrupled and doubled respectively to comprise over 19% of the total dietary volume, most of the observed difference being due to the large proportion of chironomid tissue (13%) ingested.

Specimens having an intestinal index of 3 contained smaller volumes, but very similar proportions of diatoms (11%) and filamentous algae (26%) to specimens having an intestinal index of 2. An increased volume and proportion (56%) of macrophyte detritus was ingested by most individuals. The proportion of animal tissue ingested fell to 7%; the difference between intestinal index groups 2 and 3 being largely accounted for by a very small quantity and proportion of chironomid tissue being ingested by specimens having an intestinal index of 3 compared with specimens having an intestinal index of 2.

Specimens having an intestinal index of 4 ingested similar mean volumes per specimen and proportions of diatoms (13%) to specimens of intestinal index 3. An increased proportion of filamentous algae (34%)

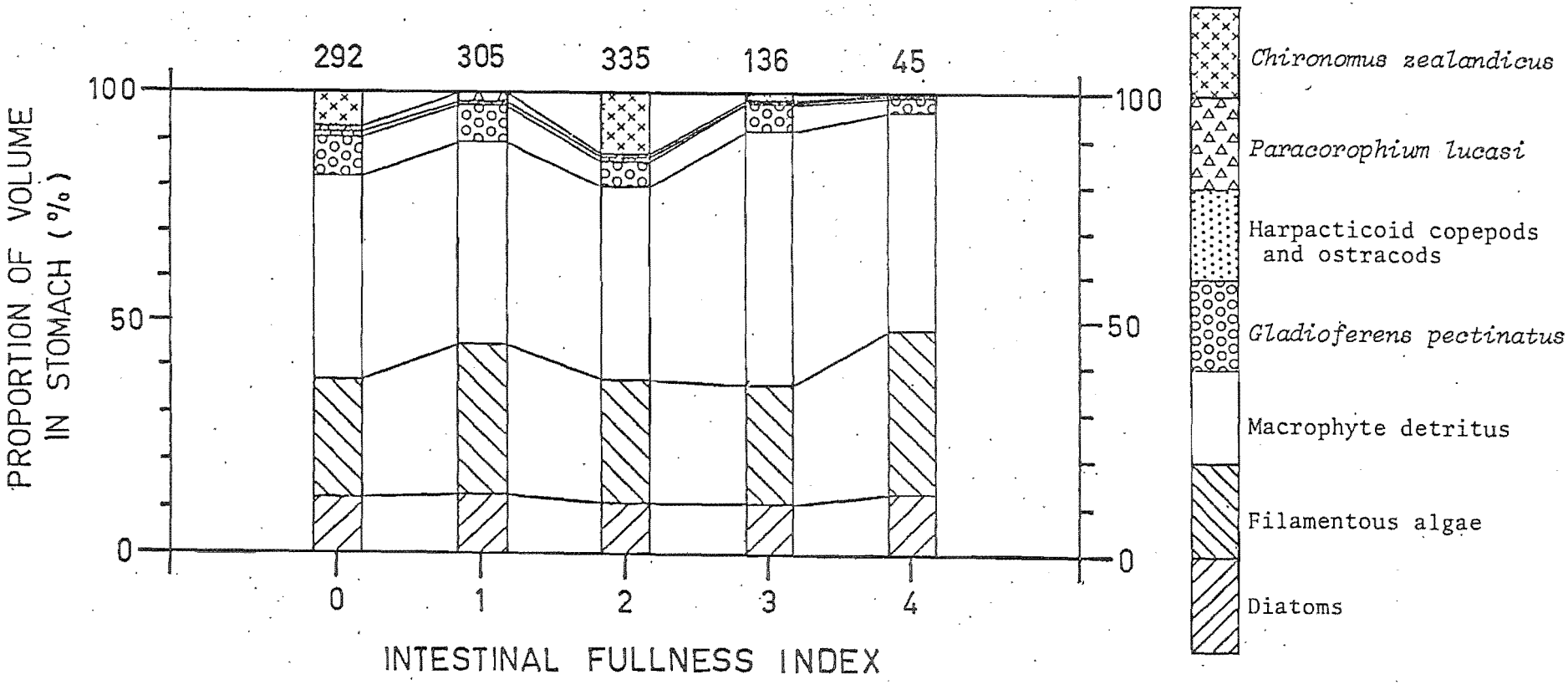

Fig. 11 Percentage composition of the diet as a function of the intestinal fullness index over the annual cycle studied. The number of specimens of each group is given at the top of each bar graph.

and decreased proportion of macrophyte detritus (49%) was ingested. The proportion of all animal foods ingested showed further reduction to 3.5%, from a maximum value of 19% for intestinal index 2 specimens, and was principally comprised of *G. pectinatus* (2.8%) and *Braniola canterburyensis* (0.5%).

The calculated volume of food present in the stomach per specimen showed a varied relationship to the value of the intestinal index. For intestinal indices of 0 to 4 the mean volume of food present in the stomach was 0.015, 0.017, 0.024, 0.024 and 0.021 cubic millimetres respectively. The intestinal feeding index does not, therefore, show a consistent relationship to the volume present in the stomach, and may not be suitable as an indicator of hunger, as the region of the intestine examined only contains partially digested foods for a brief time prior to voidance of faecal material (Molloy, 1958).

A restricted analysis of diet compared to the stomach fullness of mysids collected over the period January to May contradicted the results obtained from a similar analysis for the whole study period. Between January and May the proportions contributed by the different components of the total food volumes ingested by mysids with different stomach fullness indices were similar, with the exception of individuals with stomach fullness index). The proportions of different foods consumed by mysids of stomach fullness indices of 0-4, respectively, were: filamentous algae 29%, 16%, 13%, 12%, 19%; *Gladioferens pectinatus* 2%, 7%, 8%, 7%, 8%; and all animals excluding chironomids 6%, 13%, 11%, 13%, 13%.

In a theoretical preference order calculated from a variety of sources and inferred from variations in the foods ingested by individuals having different stomach fullness indices, filamentous algae were given a low rank (Table 4). On the same basis animal tissues should, theoretically, have been preferred

If the mysids were showing food preference decreasing proportions of algae and increasing proportions of animal tissue should have been ingested with increasing value of the stomach index (see discussion). The proportions of different foods present in mysids having different stomach fullness indices consistently showed these expected trends only when mysids of stomach fullness indices 1 and 2 were compared.

4.2.3 Influence of Stage of Development on Dietary Selection

When the diet of *Tenagomysis chiltoni* was analysed with respect to the length of each specimen examined, several differences were apparent

Table 4. The estimated calorific values, assimilation efficiencies and energy contribution of items in the diet of *Tenagomysis chiltoni*.

Food item	Calorific value ($kJ.g^{-1}$ dry wt)	Assumed assimilation efficiency	Estimated energy available per unit weight ingested ($kJ.g^{-1}$ dry wt)	Estimate of preference order
Chironomus zealandicus	17.6 (1)	82% (6)	14.4	4
Paracorophium lucasi	17.6 (2)	85% (7)	15.0	3
Harpacticoid copepods and ostracods	22.7 (3)	85% (7)	19.3	2
Gladioferens pectinatus	22.7 (3)	85% (7)	19.3	1
Macrophyte detritus	16.4 (4, 5)	20-25% (8)	<8.2	7
Filamentous algae	17.2 (5)	85% (9)	14.6	6
Diatoms	20.6 (4)	90% (10)	18.5	5

1 = Ryan (1978).
2 = *Paracalliope fluviatilis*, Ryan (1978)
3 = per g ash free wt, Cummins (1967)
4 = Cummins (1967)
5 = Cianciara (1980)
6 = Lasenby and Langford (1973)
7 = as *Daphnia pulex*, Lasenby and Langford (1973)
8 = Foulds and Mann (1978)
9 = Pechen-Finenko (1977)
10 = Clutter and Theilacker (1971)

between different 3 mm size classes. Specimens in the 2.0 - 4.5 mm length classes consumed 6% diatoms, 48% filamentous algae, 44% macrophyte detritus and 2% animal tissue (composed predominantly of *Gladioferens pectinatus*) (Fig. 12).

Within the length class of 5.0 - 7.5 mm a larger mean volume of diatoms was ingested by most individuals, forming 9% of the total ingested volume, and was composed largely of heavily silicified species also ingested, in smaller proportions, by 2.0 - 4.5 mm mysids. Smaller mean volumes of filamentous algae were ingested to form a reduced proportion of the diet (41%) compared with the shorter mysids. Macrophyte detritus was ingested in larger quantities by each individual and comprised 47% of the diet of the 5.0 - 7.5 mm length range mysids, an increase of 4% from the proportion ingested by mysids within the 2.0 - 4.5 mm length range. Animal tissues were ingested in increased proportions (3%) by these larger mysids, due to the incorporation of the amphipod *Paracorophium lucasi* into the diet in noticeable volumes.

In the length class of 8.0 - 10.5 mm specimens of spring and summer cohorts were showing secondary sexual development. Large mean volumes of diatoms (composed predominantly of the heavily silicified groups I and J) were ingested by individuals of this size, forming 17% of the total volume of food ingested, this was twice the proportion within the diet compared with mysids from the 5.0 - 7.5 mm length range. The volume of filamentous algae ingested by each individual rose slightly, but formed a much smaller proportion of the diet (27%) than in the 5.0 - 7.5 mm size class; the larger volume present in the stomach being related to ontogenetic changes in the capacity of the digestive tract. Macrophyte detritus was ingested in greater quantities than by mysids from the 5.0 - 7.5 mm length range, but contributed a similar proportion to the diet (49%). Greater quantities and proportions of animal tissue (7%), predominantly *G. pectinatus* with some harpacticoid copepods and amphipods, were ingested by this size group compared with smaller mysids.

Tenagomysis chiltoni of both sexes from the 11.0 - 13.5 mm size groups were sexually reproductive during the spring, summer and early autumn. The mean volume of diatoms ingested by each member of this size range increased marginally, however the proportion of diatoms within the diet (10%) was considerably less than in the 8.0 - 10.5 mm size range. In mysids of both these size ranges the larger diatoms of groups A, F, L, and particularly groups I and J dominated. Filamentous algae were ingested in similar volumes by individuals of the two size ranges; but the population as a whole consumed less filamentous algae as a proportion of the diet (20%).

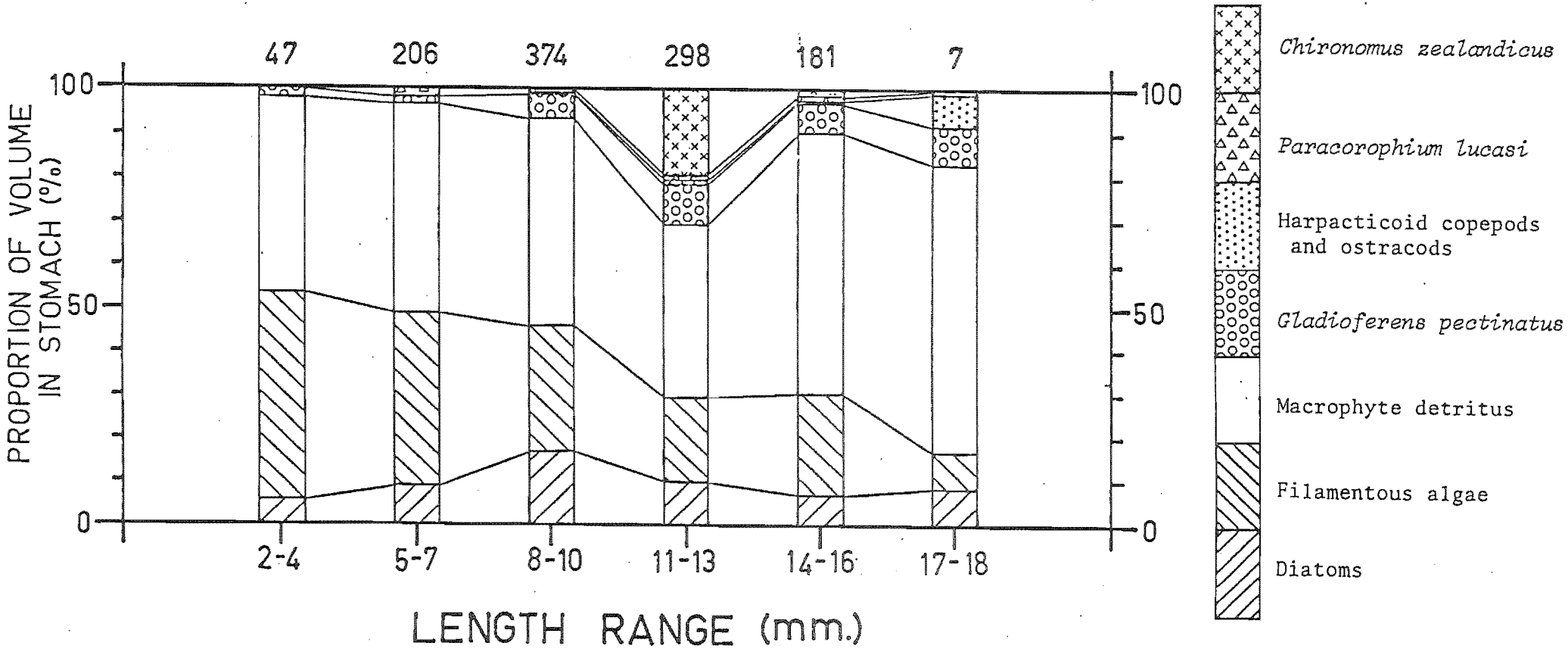

Fig. 12 Percentage composition of the diet as a function of overall length over the annual cycle studied. The number of specimens of each group is given at the top of each bar graph.

Macrophyte detritus comprised 40% of the total volume ingested; a smaller proportion, but a marked increase in the mean volume ingested. The 11.0 - 13.5 mm size range ingested the largest proportion (30%) and total volume of animal tissues. All common prey species were taken, but the greatest volumes of animal tissue ingested were of *Chironomus zealandicus* and *Gladioferens pectinatus*. The 8.0 - 10.5 mm and 11.0 - 13.5 mm size ranges contributed the largest number of specimens of any of the size groups of *T. chiltoni* ised in this study (Fig. 13).

Specimens within the size ranges 14.0 - 16.5 mm and 17.0 - 18.5 mm were predominantly overwintering adult females which had access to food resources showing decreased absolute abundance and diversity. Individuals within the 14.0 - 16.5 mm size range, and overwintering adults within the population as a whole, ingested smaller volumes and proportions of diatoms (7%) than individuals in the 11.0 - 13.5 mm size range. Smaller quantities of filamentous algae, which nevertheless constituted a larger proportion of the diet (24%) due to the smaller quantities of food within the stomachs of overwintering mysids, were ingested despite the larger mean size of *T. chiltoni* during the winter. Individuals from the 14.0 - 16.5 mm size group ingested larger quantities and proportions (60%) of macrophyte detritus than smaller mysids. Animal tissue comprised only a small proportion of the diet (9%) compared with the 11.0 - 13.5 mm size group; the difference is largely attributable to a smaller ingestion of chironomids due to the absence of the small young chironomids normally ingested by *T. chiltoni* during winter months.

The 17.0 - 18.5 mm length range comprised only seven of the 1113 specimens examined during this study. The proportions of various foods ingested by this length class were 9% diatoms, 8% filamentous algae, 66% macrophyte detritus and 17% animal tissue (principally composed of *G. pectinatus, Braniola canterburyensis* and *Gomphocythere duffi*).

The length of *Tenagomysis chiltoni* found to have ingested the amphipod *Paracorophium lucasi* was compared to the overall length of the *P. lucasi* ingested, calculated from a model II regresstion equation (correlation coefficient = 0.92) of tarsal claw length against the distance between the eye and the tip of the telson of *P. lucasi*. When all measurements of *T. chiltoni* length and calculations of *P. lucasi* length were compared using a model II regression equation, no significant correlation was found between predator and prey length (r = 0.03) (Fig. 14). However, when the analysis was restricted to the larger *P. lucasi* ingested by *T. chiltoni* of a given length, a much better fit was obtained between

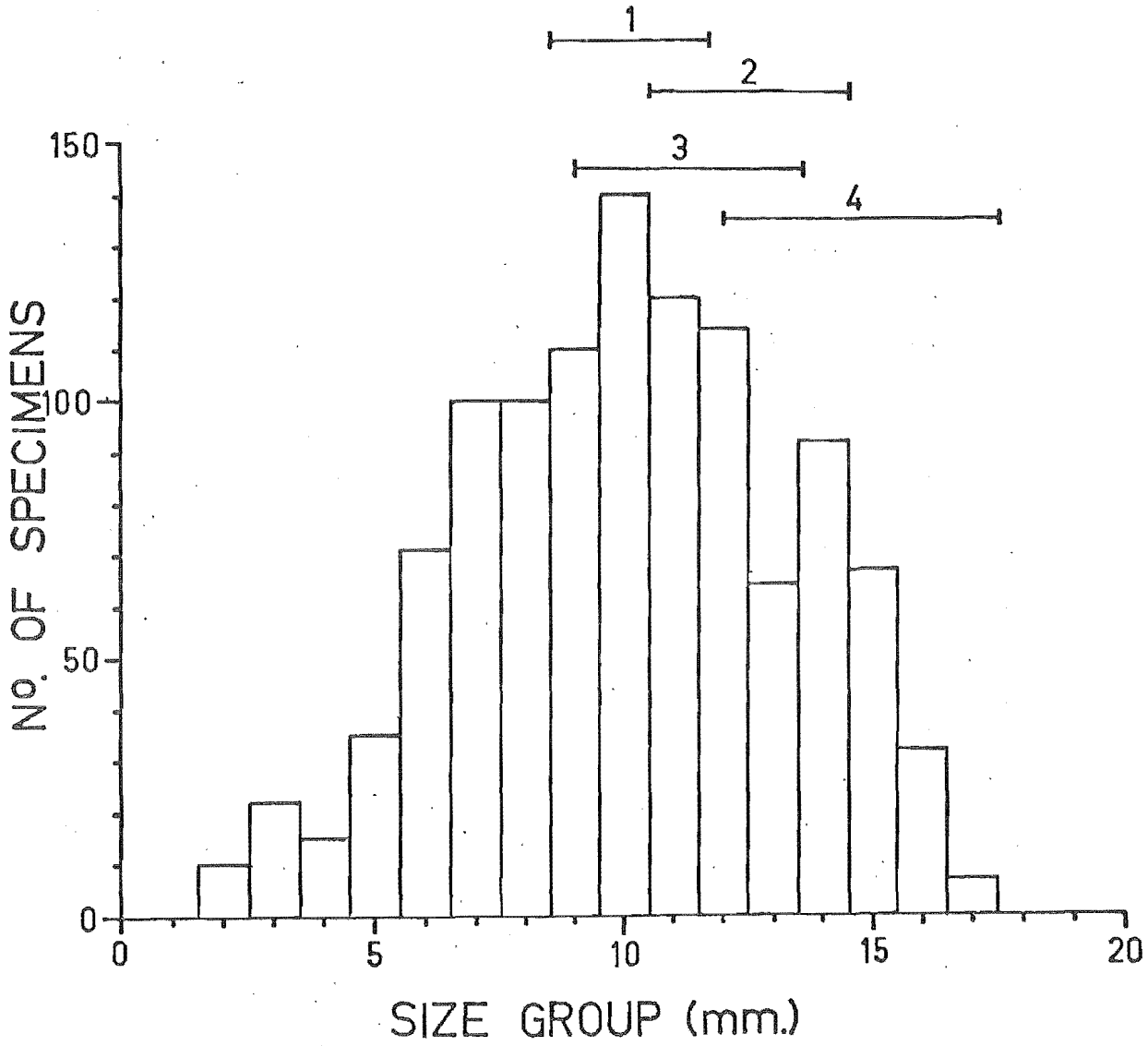

Fig. 13 Frequency of occurrence of specimens of different overall lengths used in computations of ingestion used in this study. 1 = spring and summer generation adult male length range, 2 = overwintered adult male length range, 3 = spring and summer generation adult female length range, 4 = overwintered adult female length range.

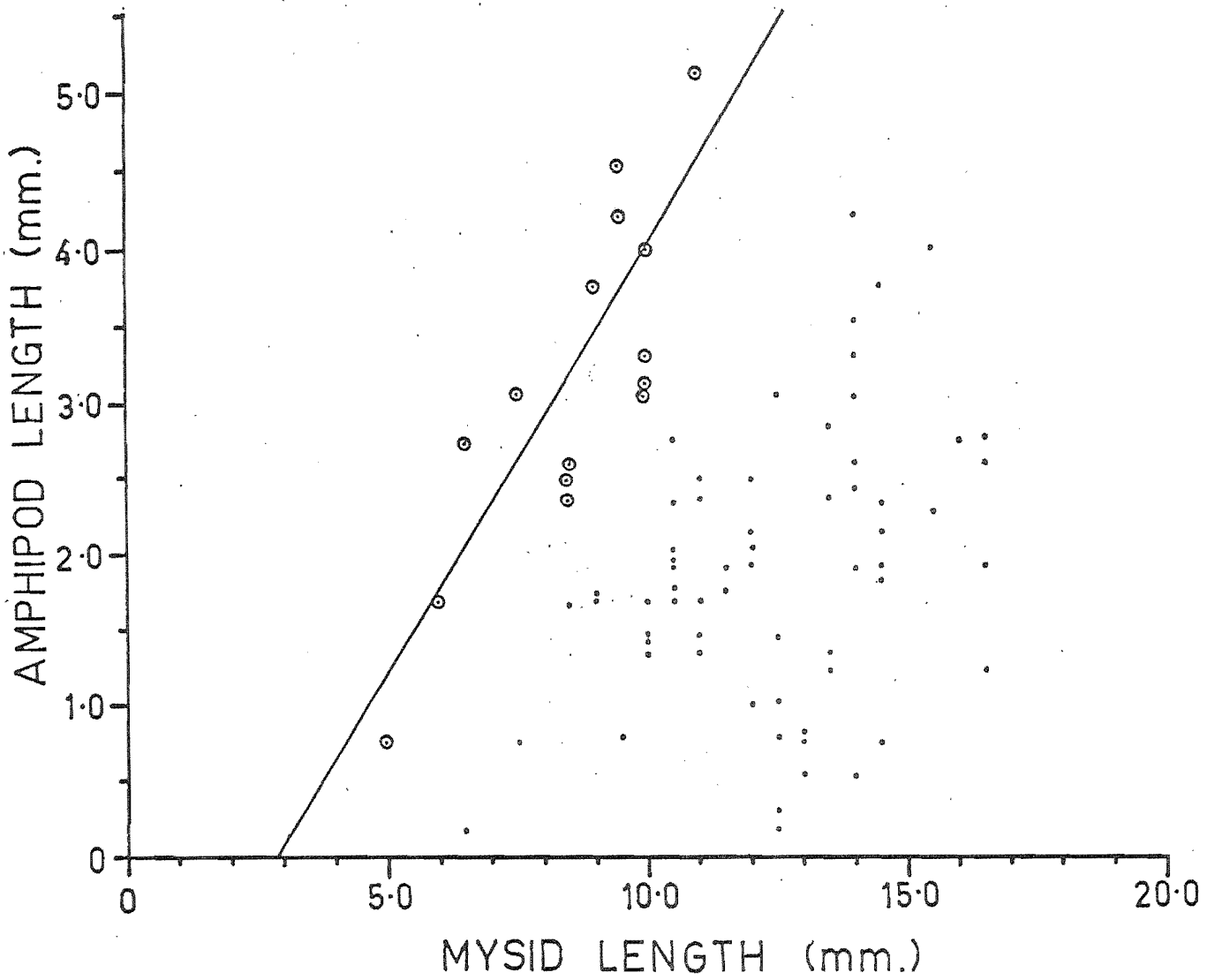

Fig. 14 The relationship between mysid lengths and lengths of the amphipod prey species *Paracorophium lucasi*. The circled points were used to calculate the plotted upper boundary regression line (r = 0.84).

the data and the calculated regression (r = 0.84). As the mysid increases in overall length from 5 mm to 11 mm the maximum length of *P. lucasi* ingested increased from 0.8 mm to 5.2 mm, which is approaching the largest size recorded for *P. lucasi* during this study and the maximum length for *P. lucasi* (5.5 mm) recorded by Chapman and Lewis (1976). Mysids larger than 11 mm appeared to ingest *P. lucasi* of all lengths, but as mysids increased in overall length from 13.5 mm to 16.5 mm a specimen of *P. lucasi* may have been rejected if its length was less than an ill-defined lower limit of from 0.3 mm to 2.5 mm. The size of *P. lucasi* ingested by *T. chiltoni* of a given length varied, but showed a slight tendency to cluster mid-way between the upper and possible lower limits, possibly as a result of the size distributions within the populations of *P. lucasi* predated upon by *T. chiltoni*.

Diet showed some relationship to the sexual classification of a specimen when results from all sampling periods were combined. Specimens of *T. chiltoni* showing no secondary sexual differentiation (juvenile) ingested a diet composed of 12% diatoms, 35% macrophyte detritus, 47% macrophyte detritus and 4% animal tissues (Fig. 15; Group 1).

Immature male specimens ingested a larger volume per individual and proportion (20%) of diatoms than the smaller juvenile group from which they were derived (Fig. 15; Group 2). Filamentous algae were ingested in similar quantities but formed a smaller proportion (28%) of the diet of the immature male group. Macrophyte detritus was ingested in larger quantities, but similar proportions (28%). The mean volume of animal tissue ingested per individual of the immature male group was twice that ingested by juvenile individuals and formed a larger proportion of the diet (6%). The animal tissue ingested consisted principally of *Gladioferens pectinatus* with small volumes of harpacticoid copepod, ostracod and amphipod tissues present, and closely resembles the composition of animal tissues ingested by juvenile individuals. No chironomid tissue was detected. On average, each immature male specimen ingested 49% more food than a neuter individual; the difference was principally attributable to differences in the modal lengths of the two groups.

Mature male specimens (Group 3) ingested similar volumes of diatoms per individual, but a slightly reduced proportion (16%) of the total volume of diatoms ingested by the population compared with immature males. Filamentous algae were ingested in slightly larger volumes and similar proportions (26%). Macrophyte detritus was consumed in smaller mean quantities per individual but in similar proportions (47%). Adult males

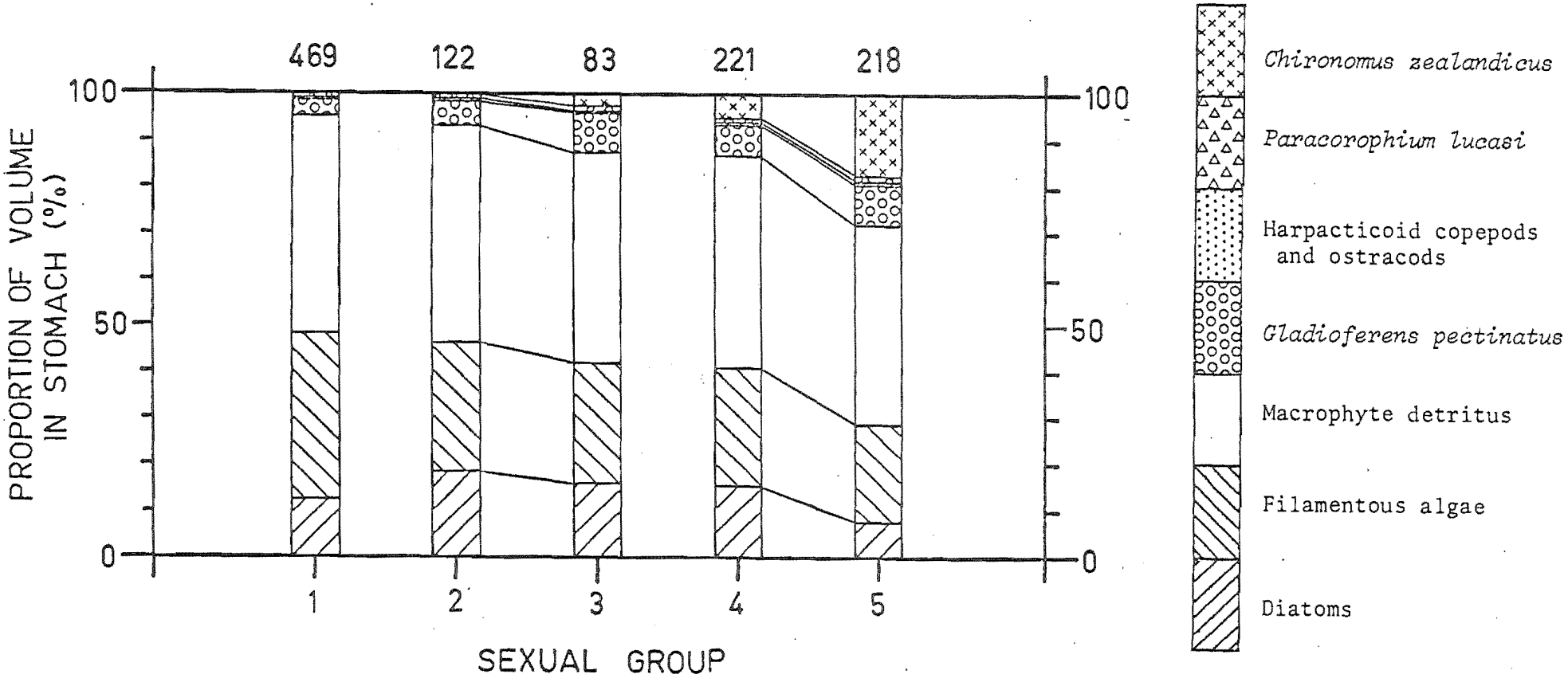

Fig. 15 The association of secondary sexual characteristics and dietary composition over the annual cycle studied. The number of specimens of each group is given at the top of each bar graph.

consumed nearly twice the volume and proportion (11%) of animal tissue when compared with immature males. The principal components of this animal tissue were *G. pectinatus* (8.5%) and *Chironomus zealandicus* (2%). Mature males ingested 34% more food than immature males, a difference largely attributable to the 2 mm difference in mean total length between the two sexual groups.

When contrasted with the juvenile group from which they were derived, immature females ingested a larger quantity and proportion (15%) of diatoms, a slightly larger quantity but smaller proportion (25%) of filamentous algae and twice the volume, but a similar proportion (47%), of macrophyte detritus. Animal tissues comprised over 13% of the total volume present and was principally composed of nearly equal proportions (6%) of *G. pectinatus* and *C. zealandicus*. Immature females ingested 2.07 times the mean volume of food ingested by juvenile individuals.

Mature females ingested a similar volume, but half the proportion (7%), of diatoms to that which immature females ingested. The volume of filamentous algae consumed was 1.19 times greater for mature females, but constituted only 20% of the total volume ingested. An increased volume of macrophyte detritus was consumed compared with immature females, but it constituted a similar proportion of the diet (46%) in all groups. Mature females ingested much greater volumes, and over twice the proportion (27%), of animal tissue compared with sub-adult females; the difference was largely accounted for by a substantial calculated ingested volume of chironomid tissue, which contributed 13% of the dietary volume. Mature females had on average 1.82 times the volume of food present in their stomachs compared with immature females.

Immature and mature female groups ingested larger quantities of food than immature and mature male groups respectively, and ingested a larger proportion of animal tissues than their male counterparts.

4.3 DISCUSSION

4.3.1 Relationship of Fullness of the Digestive Trace and Nature to Foods Ingested

In fish the nature of the ingested food depends primarily on the morphology and feeding behaviour and secondarily on the composition and amount of available food (Pillay, 1952; cited in Berg, 1979). The choice of feeding strategy employed by an animal should maximise the rate of

energy gain by the organism (Doyle, 1979; Lam and Frost, 1976; Lehman, 1976; Taghon *et al.*, 1978), maximise energy gain with the ingestion of a necessary minimum quantity of essential nutrients (Pulliam, 1975) or maximise the value of food ingested per unit time (Estabrook and Dunham, 1976). To obtain the maximum nutritional benefit from the available food resources an animal should fill the limited space available within the digestive tract with those food resources which contain the maximum extractable nutritional value in excess of the cost of the capture of the food particles. At any place at a given time a hierarchical food preference should exist if an animal is truly selective. No partial preference should exist (Pulliam, 1974) and no foods richer than those present in the diet should be ignored (Estabrook and Dunham, 1976) if maximisation of net energy gain is the sole nutritional strategy. However, if nutrient constraints are operative, partial preference may exist as an organism may have to ingest foods of lower energy content which contain the required nutrient compounds (Pulliam, 1975). Few of the proponents of the energy maximisation hypothesis or of the theories advocating nutrient optimisation seem to give due acknowledgement to the fact that in a variable environment a moderate proportion of the observed, ingested material may be consumed as the result of exploratory feeding as an animal attempts to establish a data base from which it can determine the optimal preference hierarchy. The extent to which an animal such as a mysid can afford to explore is unknown, and may be limited and is possibly restricted to an examination of the benthic and water column food resources. *T. chiltoni* will rise from the bottom of aquaria if abundant suspended homogenised grass is added as a food.

To use a conceptual preference hierarchy effectively two sets of parameters must be evaluated by an animal. Firstly, the absolute and relative abundances of the available preferred foods resources to be utilised must be known (Pulliam, 1974) in terms of the capture rates attainable by an animal and, secondly, an animal must know the volume immediately available within the digestive tract for the processing of additional ingested nutritional materials. When these factors have been assessed an animal can select which of the range of preferred foods to ingest on the basis of available processing capacity and the rate at which it can supply raw materials of various nutritional values.

A fish which is approaching satiation feeds differently from a fish which is hungry (Elliott and Persson, 1978); organisms closer to satiation should select more strongly for the richer food particles present to fill

the more limited space within the digestive tract (Emlen, 1966; Estabrook and Dunham, 1976). The proportions of any preferred foods should therefore increase with increasing nutritional value, partially excluding foods lower in the preference hierarchy. Behavioural selection of foods by insects has been recorded (Cianciara, 1980; Dethier, 1970).

One dimension of hunger may be defined on the basis of the rate of food assimilation divided by the gut volume (Holling, 1965) or alternatively as the proportion of the total stomach volume filled with food (Windell, 1978; Vahl, 1979). In fish the stomach wall stretch receptors inhibit the feeding centre in the hypothalamus when little space is available in the stomach, resulting in decreased ingestion (Vahl, 1979). The rate of food ingestion is related to the volume of food being processed; a parameter more accurately measured using the intestinal fullness index value than the stomach fullness index value as it is independent of food retention behind the stomach filter. These are operational definitions of hunger and do not take into account specific hungers, mentioned by Carefoot (1973), Dethier (1967, 1970), Lat (1967) and others, which appear to exert an influence on dietary regulation through metabolite monitors (Dethier, 1970; Harper, 1967; Vahl, 1979).

The demonstration of a preference hierarchy in *Neomysis mercedis* (Edmondson and Murtaugh, 1980) suggests that either selective feeding of a physical nature occurred, or that preferential ingestion of optimal diet components occurred, or that both occurred synchronously. If preferential selection of available food resources is a strategy employed by *Tenagomysis chiltoni*, a correlation of the nutritional value of the foods ingested with the stomach and/or intestinal feeding indices may be expected. The nutritional value of a given food resource is dependent not only upon its calorific value, as some proponents of the energy maximisation hypothesis appear to advocate, but also upon the physical and chemical structure of the food particle and the consuming organism's ability to break down physico-chemical barriers to digestion. Calorimetry alone is an inadequate means of determining food values; calorimetry based on dry weight gives a value unrepresentative of the nutritional value of a food per unit volume of digestive tract occupied, the value of interest to an energy optimising organism. A more comprehensive consideration of the biochemical composition of each component of the diet, the availability of biochemical components to a consumer, the inherent potential of an animal to evaluate nutritional composition and other factors affecting the overall desirability of each food material is necessary to assess the value of a dietary item.

There is little information concerning any of the above parameters available for *T. chiltoni* or its food organisms within the Lake Ellesmere system, with the exception of fourth instar *Chironomus zealandicus* larvae which had a calorific value of 17.6 $kJ.g^{-1}$ dry wt (Ryan, 1978), calorific values have had to be derived from various sources within the literature (Table 4).

No assimilation efficiencies have been calculated for components of the diet of *T. chiltoni*. Mysids in other systems have attained high assimilation efficiencies when fed various animal tissues (chironomid larvae, 82%; *Daphnia pulex*, 85%: Lasenby and Langford, 1973), 'phytoplankton' (unspecified, 90%: Clutter and Theilacker, 1971) and algal foods (unspecified, 85%: Pechen-Finenko, 1977). Digestion and absorption of most living food materials therefore seems to be uniformly high. The high assimilation efficiencies obtained for mysids feeding on filamentous algae are possibly partly dependent upon high cellulase activities, demonstrated in *Mysis stenolepis* by Foulds and Mann (1978). The assimilation efficiency of *Mysis stenolepis* digesting detritus made from sterile hay was lower than that on sterile hay (20-30%) or sterile cellulose (30-50%), contrary to assumptions that conditioning of plant materials by micro-organisms enhances their food value to consumers, at least in energetic terms (e.g., Anderson and Sedell, 1979; Burkholder and Bornside, 1957; Fenchel, 1970, 1972; MacGinitie, 1935; Teal, 1962; Zo Bell and Feltham, 1942). This is probably due to high concentrations of refractory materials in the hay detritus (Foulds and Mann, 1978). Because of the high concentration of lignin-like compounds which are relatively indigestible (Hargrave, 1970) and the presence of other structural compounds in hay that are resistant to digestion, the assimilation efficiency attained on sterile hay is probably not representative of the assimilation efficiencies achieved by *T. chiltoni* on the marsh grass detritus present in Lake Ellesmere, as the loss of non-structural carbohydrates is rapid during the conditioning process (Godshalk and Wetzel, 1978). The high assimilation efficiency of *M. stenolepis* digesting raw cellulose (30-50%) suggests that the assimilation efficiency of mysids ingesting grass detritus may be relatively high even for much decomposed grasses. In the case of plant detritus, however, the energetic value of the material ingested will be influenced by its phylogenetic origins (Anderson and Sedell, 1979; Gasith and Lawacz, 1976), the effect of age and thermal histories on the decomposition rates of the different types of particles present (Burkholder and Bornside, 1957; Sutcliffe, Carrick and Willoughby, 1981) and physical

structure (Burkholder and Bornside, 1957; Fenchel, 1970; Hargrave, 1970; Newell, 1965; Sutcliffe *et al.*, 1981). These factors exert an unknown influence on the conditioned detritus, and show considerable variation between different components of the macrophyte detritus food resource. As these factors were not investigated in the present study, the energetic and nutritional value of marsh grass detritus to *Tenagomysis chiltoni* was estimated using calorific values from the literature (Cianciara, 1980; Cummins, 1967) and the range of assimilation efficiencies reported by Foulds and Mann (1978).

The calculated energy utilised per gram dry weight of tissue consumed for all animal tissues consumed was between 14.4 $kJ.g^{-1}$ and 19.3 $kJ.g^{-1}$, assuming assimilation efficiencies of 82-85% (Table 4). The energetic value of macrophyte detritus to *T. chiltoni* was probably less than 8.2 $kJ.g^{-1}$ dry wt. Filamentous algae contributed 14.6 $kJ.g^{-1}$ and diatoms contributed 18.5 $kJ.g^{-1}$ to *T. chiltoni* after digestion.

The energy contributed per unit dry weight of food is an unsatisfactory method of estimating food value, as commented earlier, because it fails to account for several parameters of "interest" to a consumer. As the amino acid compositions of animal foods are probably more similar in their amino acid compositions to tissues of *T. chiltoni* than that of plant foods, animal foods have been placed higher in the estimated order of preference than diatoms (Table 4). Diatoms are captured by filtration; the cost of capture is therefore high, offsetting their high calorific value in terms of net energy gain (Lam and Frost, 1976). The calorific value of diatoms used is also higher than the values given by Werner (1977).

When dietary composition is examined on the basis of the value of the stomach fullness index in all samples, some changes in the proportions of the various components of the diet between stomach index 0 and 4 are found (Fig. 10). In particular, the proportions of all animal tissues ingested, i.e., the combined totals of the four highest ranked prey types, increased from 5% to 29% of the total volume ingested, though the contribution of each prey type was very variable. The proportion of diatoms ingested also increased markedly between mysid groups having a stomach fullness index of 0 and 1 (from 4% to 12%), and thereafter showed modest increase to comprise 14% of the total volume of food present in the stomach of mysids having a stomach fullness index of 4. As diatoms were estimated to be only moderately preferred, this result is consistent with the hypothesis that *T. chiltoni* was feeding more selectively when well fed

than when the stomach was less full. When the proportions of the two commonly ingested food categories lowest on the preference order (filamentous algae and plant detritus) are examined, their combined contribution to the diet is noticeably higher in stomach index 0 individuals (91%) than stomach index 4 individuals (57%). This observation is consistent with a hypothesis that less beneficial dietary components are rejected by nearly sated mysids. In individuals having stomach indices of 1, 2 and 3, the combined contribution of macrophyte detritus and filamentous algae was similar. However, a progressive reduction in the proportion of filamentous algae ingested was observed between groups of individuals having stomach index values of from 1 to 4. The contribution of macrophyte detritus was only slightly variable over the whole range of stomach feeding indices. This suggests that macrophyte detritus may have been preferred to filamentous algae by *Tenagomysis chiltoni*, and not as suggested in Table 4. Macrophyte detritus was selected in preference to filamentous algae as a food of the mayfly *Cloeon dipterum*, and was considered to be a higher quality food as it produced a higher growth rate despite its lower calorific value (Cianciara, 1980). It is possible that an increase in the quality of detritus may result from the addition of nutrients of microbial origin during the conditioning process (Anderson and Seddell, 1979; Fenchel, 1970, 1972; Teal, 1962). This is contrary to the results of Foulds and Mann (1978), who show that decomposition of straw detritus decreased the efficiency with which *Mysis stenolepis* incorporated its carbon content. When the results are viewed as a whole they give consistent support to the theory that *Tenagomysis chiltoni* becomes increasingly selective with increasing satiation.

When the proportional composition of the diet of individuals having different intestinal feeding indices were compared, a far more confused pattern emerged (Fig. 11). No consistent trends towards reduction or increase in the proportion of diatoms, filamentous algae or macrophyte detritus were evident. Ingestion of animal tissue was greater at median and low intestinal fullness indices than at the highest indices, but results were variable. Molloy (1958), working on several species of mysids, stated that partially digested foodstuffs entering the hindgut were rapidly voided by peristaltic contractions. If the physiological process is identical in *T. chiltoni*, an inconsistent relationship between an individual's intestinal fullness index and either the proportional composition of the diet or the total volume of food ingested could be expected; a consistent relationship is found in neither case. There is, however, a good

relationship between the stomach fullness index and the total volume of food ingested. This suggests that the lack of association of dietary changes between different intestinal fullness index values and the estimated preference hierarchy is associated with a short retention time of digested food material within the region of the intestine studied, rather than a lack of the dietary selectivity consistently exhibited when making similar comparisons on the basis of an individual's stomach fullness index. It also suggests that regulatory mechanisms controlling appetite are absent from the hind gut of *T. chiltoni*.

Post-ingestive dietary regulation has been discussed by numerous authors (e.g., Dethier, 1970; Elliott and Persson, 1978; Holling, 1965), and been shown to operate through sensors of stomach fullness in fish (Vahl, 1979; Windell, 1978). Very little is known about the digestive capacity of aquatic insects (Cummins, 1973). In *T. chiltoni* the utilisation of the available digestive capacity may be influenced by sensors of stomach fullness as a consistent relationship was found between stomach fullness and apparent dietary selectivity using a stomach fullness index based on subjective observational data supported by calculated total food volumes, however the results of the same analysis restricted to four months contradict this statement. Whatever the mechanism controlling hunger, it is only relevant to this study through its effect on feeding behaviour (Beukema, 1968), which was indefinite.

The analysis designed to exclude the most pronounced seasonal influences, and also variability in the calculated ingestion of *Chironomus zealandicus*, failed to demonstrate a consistent effect of hunger upon the food preference of *T. chiltoni*, as found in the mayfly *Cloeon dipterum* (Cianciara, 1980). Subsequent references to dietary selectivity and preference refer to physical mechanisms of selection as described, for example, by Cannon and Manton (1927), operating as a determinant of the probability of capture of a particular food particle (Boyd, 1976). It is concluded that preferential feeding by *T. chiltoni* is, at most, of little significance to its diet selection within Lake Ellesmere and that apparent selection in other mysids (see Edmondson and Murtaugh, 1980; Rybock, 1978) is most probably a phenomenon occurring as a result of the physical structure of the feeding mechanism interacting with the environment. The "overwhelming preference" of a mysid probably does not involve active choice, but may be explained by strictly mechanical considerations (Edmondson and Murtaugh, 1980). Another explanation is given by Carefoot (1973), who concluded that the preferences of the isopod *Ligia pallasii* were related to food availability rather than preference.

4.3.2 Influence of Stage of Development on Dietary Selection

Many factors may cause dietary changes associated with age but most of them cannot be demonstrated using the generalised techniques used in this study. The early stages of most Crustacea are dependent on parental energy reserves during their early life (e.g., Gauld, 1959), and recently released *T. chiltoni* appear to carry a small residual quantity of yolk and may therefore be less dependent upon ingested foods during early post-larval stages. As a crustacean grows it may experience size-specific changes in filtration and ingestion rates (e.g., Brooks and Dodson, 1965; Burns, 1969; Burns and Rigler, 1967; Kato, Murano and Segawa, 1979; Newell and Northcroft, 1965; Nash, 1974) which may not be proportional to changes in the size of the animal (Kato *et al.*, 1979; Mullin and Brooks, 1970; Randlov and Riisgard, 1979). As the size of the animal increases, its ability to handle larger food sources may also increase (e.g., Fahy, 1972; Gray and Ward, 1978; Howard and Scott, 1959; Mauchline, 1967; Moore, 1977; Nival and Nival, 1976; Nybakken and Eastman, 1977). Large size is not necessarily associated with carnivorous habits (Muttkowski and Smith, 1929), however, Siegfried and Kopache (1980) found that *Neomysis mercedis* ingested only small amounts of animal tissue when under 4 mm in length (their Figure 4) but that immature mysids (7 mm in length) and mature mysids (11-12 mm in length) ingested substantial proportions of animal tissues, principally of copepods. Edmondson and Murtaugh (1980) found that larger *N. mercedis* ingested more animal prey of larger sizes than did small mysids. Developmental differences in specific nutrient requirements may also occur (Lat, 1967).

When the diet of 3 mm length groups of *Tenagomysis chiltoni* is examined, we find that with increasing size up to 10 mm total length an increasing proportion of diatoms, especially the large and more siliceous forms, were ingested. The increasing preference for large more siliceous forms may result from an increased ability to masticate the stronger frustules or from the development, with increasing size, of the ability to ingest larger particles (Cannon and Manton, 1927). Nival and Nival (1976) showed size selectivity changes between copepodite stage 1 and adults of the copepod *Acartia clausi* resulting from changes in intersetular spacing on the maxilla which occurred without fundamental structural modification of the appendage. As small *T. chiltoni* collect diatoms living as disassociated individuals, it appears that their filter mechanism is also capable of collecting larger cells, such as those within Groups I and J, about 100 µm in diameter. Larger algal foods produced faster growth rates in *Euphausia pacifica*, but there was little difference in growth

rates between groups fed on unialgal or mixed algal cultures (Ross, 1981), suggesting that differences in growth rates were not attributable to increased dietary diversity as was suggested by the work of Mullin and Brooks (1970). The faster growth rates are probably attributable to an increase in the amount of food collected per unit energy expended in feeding activity (Lam and Frost, 1976). In the 11-13 mm size range, a smaller proportion of diatoms was ingested, apparently associated with the ingestion of large quantities of animal tissues. The 14-16 mm size group ingested a smaller quantity and proportion of diatoms even in the absence of the ingestion of marked quantities of animal tissue. This is principally a superimposed seasonal phenomenon rather than a size-selective one, and was brought about by the decreasing quantities of diatoms available over the winter months which these largest overwintering *T. chiltoni* were present (see Chapter 5).

The overall proportion of animal tissues ingested increased exponentially with increasing mysid size up to 13 mm in length, but larger overwintering mysids ingested a smaller percentage of animal tissues due to a lesser abundance of animal food resources over the winter months, possibly accentuated by decreased foraging activity of mysids as a consequence of lower water temperatures. The calanoid copepod *Gladioferens pectinatus* was the principal source of ingested animal tissue, comprising 6% of the total volume of food ingested by all the mysids sampled. *G. pectinatus* formed an increasingly important source of food for larger mysids up to 13 mm in length, and in larger animals *G. pectinatus* still contributed substantially to the diet of *T. chiltoni*, but comprised a smaller proportion of the diet as a consequence of decreased abundance during winter months. *Chironomus zealandicus* was the second most important source of animal food for *T. chiltoni*, but only contributed substantially to the diet of mysids between 11 and 13.5 mm in length, for which chironomid tissue formed nearly 20% of the total volume ingested, although chironomid tissue was also ingested in small quantities by mysids 14 mm in length. The ingestion of chironomid tissue occurred only in the largest mysids present during spring and summer. The *C. zealandicus* larvae ingested were of the smallest size class found in Lake Ellesmere, i.e., early instar larvae; the ingestion of *C. zealandicus* tissue is therefore partially dependent on the reproductive pattern of the chironomid. Amphipod, harpacticoid copepod and ostracod tissue occasionally contributed substantial volumes to the diet of individual mysids, but on average was consumed in small proportions by all length groups. The few mysids

17-18 mm in length ingested unusually large quantities of harpacticoid copepods and ostracods during the winter months, a phenomenon not shown by other size classes. Minimal quantities of the smallest available amphipod *Paracorophium lucasi* were taken by mysids less than 8 mm in length. Only the smallest prey items were ingested by the 2-4 mm and 5-7 mm animals, but as the mysids grew they fed with increasing intensity upon the larger animal foods present and also ingested larger quantities and proportions of the smaller animals present. Larger specimens of *T. chiltoni* consequently ingested a greater proportion and diversity of animal prey with increasing size, as found also by Nybakken and Eastman (1977) in their study of the food preference of the nudibranchs *Triophia maculata* and *T. carpenteri*. Many authors record the influence of predator size upon the nature of the food ingested (e.g., Fisher and Goldie, 1959; Macdonald, 1927; Menge, 1972; Sheldon, 1969). Anderson and Sedell (1979) stated that some species of aquatic detritivore switch to a more predatory lifestyle as they age, and Gray and Ward (1978) recorded this phenomenon in a stonefly *Isoperla patricia*. Edmondson and Murtaugh (1980) showed that small *Neomysis mercedis*, the only other mysid species examined for ontogenetic changes in diet, only ingested the smallest available cladocera and did not ingest a rich potential copepodite food resource. *Tenagomysis chiltoni* did ingest copepodite and adult *Gladioferens pectinatus*, but in considerably reduced proportions with respect to the available food resource. Copepodites comprised only 4% of the calculated volume of *G. pectinatus* tissue ingested by *Tenagomysis chiltoni*. Mauchline (1967) stated that harpacticoid copepods were ingested by the larger *Schistomysis spiritus* present; *T. chiltoni* of all sizes consumed copepods, but the proportion consumed increased as the mysid grew.

The proportion of detritus consumed by mysids of increasing size remained remarkably constant up to 13 mm total length; over the same increase in length the proportion of filamentous algae in the diet was progressively reduced from 48% to 20%, and the proportion of animal foods increased markedly. Mysids of greater length were also present during months in which filamentous algae became less abundant, within the water column food resource from which *T. chiltoni* feeds (see below), and at times when animal prey were more abundant. Part of this change in diet with growth may therefore be of a seasonal nature. However, post-larval mysids ignore animal prey taken by adults at the same site, suggesting that real size selection occurs. Similar amounts of filamentous algae and diatoms were ingested by the 11-13 mm and 14-16 mm size groups, but ingestion

of filamentous algae by the largest overwintering mysids (17-18 mm length range) was less than in any other length group which probably partly reflects seasonal availability.

The mean volume of food collected showed a slight exponential increase with increasing total length up to 13 mm. During the winter the effects of the poorer food resource, and possibly lower water temperatures, on the ingestion rate of *T. chiltoni* caused a decline in the rate of increase.

A comparison of the length of a single species of prey, *Paracorophium lucasi*, with the length of the mysid which ingested it, demonstrated that the maximum prey size handled was a function of predator length up to the maximum observed size of *P. lucasi*. This relationship was found also in *Neomysis mercedis* which attacked the largest prey taken less efficiently (Edmondson and Murtaugh, 1980). It was not clear whether mysids ingested all sizes of amphipod up to the maximum prey size for mysids of a given length, or whether the largest mysids did not ingest the smallest amphipods present. As the mysids successfully trapped and ingested copepods of shorter lengths and smaller volumes than the amphipods which may have been rejected, this seems unlikely. Many authors report a correlation between the size of a single species of prey and the predator which consumed it (e.g., Fahy, 1972; Houston, 1973; Menge, 1972; Moore, 1977), including a study of mysids (Edmondson and Murtaugh, 1980), and several note that a lower limit to the size of prey that was ingested by a predator of a given length existed. *Hemimysis lamornae* of different lengths may ingest different optimal size ranges of particles (Cannon and Manton, 1927).

Developmental changes during sexual development result in changes in calorific values of a mysid (Johnson, 1978), and may result also in changes in specific appetites necessitated by ontogenetic changes in the biochemical composition of the body tissues. Changes in the composition of the nutritional material ingested, particularly of animal tissues, may therefore reflect developmental alterations in the physiological requirements of the organism, as well as changes in the dimensions of structures during ontogenetic development facilitating prey capture. As *T. chiltoni* could not be shown to be an optimal feeder this is not an effect of choice.

When the proportion of foods ingested by animals of different secondary sexual development is examined, we find a similar proportion of macrophyte detritus is ingested by all groups. The total proportion of living plant material ingested decreases progressively between juvenile

and sub-adult, and sub-adult and adult, members of each sex and a concurrent increase occurs in the proportion of animal tissues ingested. This suggests that live plant materials, primarily filamentous algae but also possibly diatoms, between sub-adult and adult groups of the same sex are displaced from the diet by the ingestion of larger quantities of animal tissues. The changes observed in the source of the animal tissues ingested by juvenile animals, and sub-adults and adults of the same sex, were probably brought about by the size differences observed between sexual groups. With the increased degree of sexual development and growth associated with ageing, larger quantities of each animal food were taken and larger forms of prey were overpowered and consumed. A difference in the proportions of animal foods consumed, and an associated decrease in the live plant fraction of the diet, occurred between females and males. Both sub-adult and adult females ingested over twice the proportion of animal tissue ingested by their male counterparts. This was almost exclusively of chironomid tissue. The difference in the amount of chironomid tissue ingested is probably explained by the moderate length differences (*ca.* 2 mm) between males and females. Males ingested only 69% and 52% of the volume of food ingested by female sub-adults and adults respectively.

Raymont and Gross (1942) recorded that male *Calanus finmarchicus* fed less actively and produced fewer faecal pellets in the laboratory. The results of this study suggest that in *T. chiltoni* the difference observed could also have been produced by the females feeding more voraciously. Nybakken and Eastman (1977) found marked differences in the diets of immature and mature individuals of *Triopha maculata* and *T. carpenteri*, in *T. chiltoni* developmental changes in diet were moderate. Decreased feeding by adults may occur through sexual immobilisation (Menge, 1972). The sexual differences in the volumes of food ingested may be a product of increases in the quantity of food consumed by females or, as noted in Chapter 2, a general decrease in the time males spent feeding in order to maximise breeding success in a limited breeding season, or a combination of both influences.

Absorption efficiencies of elm leaf detritus varied between 36% and 59% in the amphipod *Gammarus pulex*, decreasing with increasing body weight (Sutcliffe *et al.*, 1981). If the digestive efficiencies of gastrointestinal processes in mysids are subject to ontogenetic changes then not only the effect of observed dietary changes are difficult to interpret. However, marked ontogenetic changes were not apparent in changes observed in the diet of *T. chiltoni* with increasing length or

sexual maturation. Where changes in diet did occur they appeared to be attributable to changes in the abundance of food resources, or in the apparent perception of these food resources by *T. chiltoni*. Mauchline (1980) cites Pasternak's (1977) study which showed a decrease in the proportion of assimilated foods invested in growth (K_2) with age. The value of K_2 decreased from 70-80% in post-larvae to 15-30% in adults of *Neomysis mirabilis*. Higher K_2 values, and possibly specific relative absorption efficiencies, in younger mysids explain the rapid growth and development of juvenile *Tenagomysis chiltoni* to maturity without ingesting larger quantities of food, or more nutritional foods. Most of the energy accumulated by mature *Mysis relicta* went into propagation (Hakala, 1979), which is probably the explanation of lower K_2 values of adult *N. mirabilis*.

Specimen size may exert a greater influence than taxonomic classification on ingestion by some cladocerans (Nadin-Hurley and Duncan, 1976). Size-related changes in dietary selection of prey by *T. chiltoni* suggest that care must be taken in defining those food resources which are potentially available to *T. chiltoni*. Prey availability is defined within the limitations of potential predators (Charnov *et al.*, 1976), which is dependent on parameters of the predator, prey and habitat, and is not a constant feature of predator prey interactions between species (Rybock, 1978). For *Tenagomysis chiltoni* size was a parameter which affected the ingestion by individuals and populations. It exerted an influence on the range of prey available to a mysid, affecting both the range of prey species taken, and the size of *P. lucasi* consumed. None of the other individual variables investigated was shown to exert an influence upon the types of food ingested by *T. chiltoni*. *T. chiltoni* did not show food preference. The degree of dietary specialisation observed is limited by the availability of food in the habitat of an animal (Emlen, 1968), and must therefore be assessed in relation to the observed food resources.

Evolution produces blends of suitability determined by several factors (Carefoot, 1973); the observed differences in the diet of *T. chiltoni* at different stages of development may reduce the intensity of intraspecific competition (Nival and Nival, 1976; Sheldon, 1969), this is not always the case however (Neill, 1975). Within Lake Ellesmere food was never observed to be a limiting factor to the development of the population of *T. chiltoni*. Neither were the observed developmental changes in diet pronounced. Therefore, this factor is unlikely to affect the degree of intraspecific competition of *T. chiltoni* in Lake Ellesmere; in habitats having less abundant, or different, available food resources it may play a more important role.

CHAPTER 5

THE INFLUENCE OF SOME EXTERNAL FACTORS ON THE DIET OF *TENAGOMYSIS CHILTONI*

5.1 INTRODUCTION

Seasonal changes in the diets of members of the Order Mysidacea have been investigated only for *Neomysis mercedis* (Mauchline, 1980). Ingestion by *N. mercedis* varied between different sampling periods and sites (Kost and Knight, 1975; Siegfried and Kopache, 1980), and reflected vulnerability of prey items to capture, rather than true selectivity (Siegfried and Kopache, 1980). *Neomysis mercedis* showed changes in electivity over the manageable size range of prey, showing that mysids may alter their feeding behaviour in response to changing availability of prey (Edmondson and Murtaugh, 1980). A high correlation coefficient ($r = 0.895$) was calculated between prey density and the extent of predation by *Mysis relicta* (Rybock, 1978). Lasenby (1979) also showed a correlation between prey density and ingestion rate of *M. relicta* over a wide range of prey densities. From the limited data available, the ingestion of mysids appears to be influenced by selectivity, and density and vulnerability of potential prey items, all of which may fluctuate seasonally. In this chapter the nature of the food ingested by *T. chiltoni* is related to the nature of the availability of potential foods.

No systematic study of the invertebrate fauna or benthic flora of Lake Ellesmere has been made previously and also no assessment of the role of macrophyte detritus within the lake. Much of the material present here is therefore of interest as a preliminary survey of a limited region of the littoral zone of Lake Ellesmere. In this context it should be noted that the data collected has been presented to show the availability of potential foods, not the abundance of the different organisms present. Organisms present but not normally ingested are not mentioned as their inclusion could create anomalous results (e.g. Gray and Ward, 1978).

Developmental changes in the morphology and physiology of a mysid may expand the range of manageable prey sizes both within a prey species and to include more prey species (Edmondson and Murtaugh, 1980); the population structure of the mysid population present must therefore be related to the information given in the previous chapter in order to define

available food resources. The availability of a food resource to an animal may vary between identical food resources as the ability to ingest a food particle is dependent on morphological and physiological constraints and this should be borne in mind while examining the experimental results.

Food resource utilisation is a composite phenomenon dependent on an interaction between the ability to ingest, the opportunity to ingest and the behaviour of an animal. In this chapter the influence of the opportunity to ingest upon ingestion is examined. This opportunity may produce pronounced variation in the life-history of *Mysis relicta* between localities (Morgan, 1980) and even in the same locality in different years (Olsen, 1980).

5.2 RESULTS

The techniques used to calculate the volumes of the different materials ingested by *Tenagomysis chiltoni* appear to have produced consistent results with three exceptions. Firstly, the method of estimating the volume of filamentous algae in the benthic food resource produced a severe and inconsistent underestimate of the availability of filamentous algae within the substrate. This underestimate was due to the filamentous algae in Lake Ellesmere growing in clusters which blocked the apertures of the samplers used in the study. This error is unfortunate as filamentous algae were an important component in the diet of *T. chiltoni*. Secondly, the method of calculating the contribution of *Chironomus zealandicus* to the diet of *T. chiltoni* sometimes appears to indicate that an unrealistically large volume of tissue was ingested at a specific time; this is due principally to the count indicator particles for *Chironomus* representing much larger tissue volumes than count indicator particles used for any other food source. This overestimate may also be contributed to by slower gut passage rates of the chironomid fragments (Berg, 1979; Hill, 1976), or ingestion of fragments of chironomid headshells contained within the sediment. Thirdly, the highly variable nature of the benthic food resource on occasions suggested that the two sets of three sub-samples used to define this resource did not adequately represent the benthic food resource of a site. The lack of relationship between this resource as estimated and to the observed ingestion of benthic components in the diet of *T. chiltoni* suggests the further possibility that the mobility of the mysid may make food aggregations or alternative food resources which were not sampled available for ingestion (MacArthur and Pianka, 1966). These possible sources of error should be borne in mind when examining the results given below.

5.2.1 The Available and Ingested Foods of *Tenagomysis chiltoni* at Site M

In September 1979 the mysids present at Site M belonged to the overwintered generation and were between 9 mm and 16 mm in length and were showing signs of sexual development. They had ingested a diet comprised principally of macrophyte detritus (69%) with smaller amounts of diatoms, filamentous algae, the planktonic copepod *Gladioferens pectinatus*, harpacticoid copepods and ostracods (Table 5). At this time the water column food resource consisted, in decreasing order of abundance, of macrophyte detritus (52%) together with diatoms, filamentous algae and *G. pectinatus* in modest quantities. The benthic food resource also consisted mostly of macrophyte detritus (63%), with diatoms, harpacticoid copepods, ostracods and the amphipod *Paracorophium lucasi*. Clusters of filamentous algae were visible but not sampled as filamentous algae blocked the aperture of the sampler.

In November most mysids present were smaller spring generation neuter individuals of 4-7 mm in length. Per individual these contained only 0.6 times the volume of food present in mysids collected in September as a consequence of the reduction in mean length, but very similar quantities of food as a population due to an increase in population density (Table 5). These specimens had ingested a diet comprised mainly of filamentous algae (68%). No trace of animal tissue was detected in the stomach, but small quantities of unicellular chlorophytes were present. At this time the water column food resource had increased to 1.4 times the total volume of potential food tissues present per litre of water present in September, and consisted mainly of filamentous algae, whereas the benthic food resource sampled comprised mainly Amphipoda. The overall concentration of food present, available within the benthic food resource, was twice that present in September. Dense growths of filamentous algae were visible on the bottom. The reduced consumption of macrophyte detritus coincides with the increased consumption of filamentous algae (Fig. 16); these changes appear to be related to changes in the water column and benthic food supplies as well as to ontogenetic changes within the mysid population.

In December most of the mysids present were slightly larger (6-10 mm in length) and some mysids showed signs of sexual development. On average, individual mysids contained four times as much food per individual and, as a population, ten times as much food compared with results obtained in

Table 5. The proportions and changes in volume (multiplication factor) of available and ingested foods of *T. chiltoni* at Site M.

	Food Type (%)	1979			1980							
		SEP.	NOV.	DEC.	JAN.	FEB.	MAR.	MAY	JUNE	JULY	AUG.	OCT.
Water column food resource	Diatoms	28	12	12	15	16	42	22	7	3	3	9
	Filamentous algae	19	60	24	26	29	18	10	48	27	13	6
	Macrophyte detritus	52	25	64	58	51	32	65	43	66	82	85
	G. pectinatus	1	3	0	1	4	8	3	2	4	2	0
	Change in volume of food present since previous month	-	1.4	2.8	1.2	0.6	0.3	1.3	1.7	0.5	1.4	1.2
Ingested foods	Diatoms	19	5	4	-	21	7	34	30	28	25	-
	Filamentous algae	7	68	31	-	20	0.4	23	9	21	15	-
	Macrophyte detritus	69	25	65	-	54	5	34	49	48	52	-
	G. pectinatus	4	0	0.2	-	3	2	6	9	1	4	-
	Harpacticoid copepods and ostracods	1	0	0	-	2	0	1	1	0	4	-
	P. lucasi	0	0	0	-	0	0	2	2	2	0	-
	C. zealandicus	0	0	0	-	0	84	0	0	0	0	-
	Individual change in volume ingested since previous sample	-	0.6	4.0	-	0.5	3.4	0.4	0.6	0.3	1.2	-
	Size range of mysids (mm)	9-16	4-7	6-10	-	7-12	6-12	6-14	7-16	9-15	5-16	-
	Population change in volume ingested since previous sample	-	1.1	9.8	-	0.4	3.8	0.2	1.0	0.6	0.9	-
Benthic food resource	Diatoms	21	24	36	22	32	35	13	5	3	3	7
	Filamentous algae	0	0	0	0	4	3	4	3	65	2	6
	Macrophyte detritus	63	9	39	61	11	21	68	82	27	87	73
	Harpacticoid copepods and ostracods	5	7	21	5	7	9	7	4	3	3	5
	P. lucasi	11	60	4	12	46	32	8	6	2	5	9
	Change in volume of food present since previous month	-	2.0	2.1	1.2	3.0	1.1	0.8	4.3	2.9	1.0	1.4

November (Table 5). Calculations suggest that only a small proportion of this change (16%) in food volume per individual was attributable to changes in the length structure of the population; changes in population density affected the volume of food present within the population and accounts for the differences between the changes in relation with the mean food volume per individual and the mean food volume present within the population. The foods ingested in December consisted of macrophyte detritus (65%), filamentous algae, diatoms and very small proportions of *G. pectinatus* tissues (Table 5). The total estimated volume of food present within the water column and benthic food resources had increased and the increased concentration of the suspended food resource best explains most of the observed increase in individual food ingestion. The water column food resource was composed also mostly of macrophyte detritus (64%) with filamentous algae, diatoms and very small volumes of *G. pectinatus* tissue. The benthic food resource was composed of almost equal proportions of macrophyte detritus and diatoms, together with harpacticoid copepods, ostracods (mainly *Gomphocythere duffi*) and the amphipod *Paracorophium lucasi*; filamentous algae were present but not sampled. The diet of *T. chiltoni* therefore resembled the composition of the water column food resources rather than the benthic food resources.

No mysids were present at Site M in January 1980. The water column and benthic food resources were, however, similar in composition to December and contained increased quantities of food tissues. The absence of mysids from this station was not therefore attributable to change in the availability of food.

In February the mysids present were 7-12 mm in length and some were actively reproducing. The population ingested less, both per individual (51%) and as a population (42%), than at the same site in December despite an increase in mean length since December. The diet consisted mostly of macrophyte detritus with diatoms and filamentous algae in approximately equal proportions (Table 5). The water column food resource contained relatively more Copepoda tissue, but a smaller volume of total suspended foods due to the calm condition of the lake in this sheltered site. It was comprised of, in decreasing order of abundance, macrophyte detritus, filamentous algae, diatoms and *Gladioferens pectinatus*. The benthic food resource contained three times the quantity of food tissue per litre of substrate compared with January and apparently was not therefore responsible for the decrease in the quantity of food ingested per individual. The depleted suspended food resource appears to have caused a reduction in the

quantity of food ingested, but the apparent reduction in ingestion rate may be caused by faster gut passage rates as a result of increased water temperature. The benthic food resource was composed mainly of amphipods and diatoms (Table 5).

By March most of the mysids present were 6-12 mm in length and many were sexually active. The calculated volume of food per individual and for the population had increased by over three times since February (Table 5). This was due to the presence of several large chironomid mandibles in the stomachs of four mysids and, although the result could be proportional to the volume of food ingested, it is probably at least partly an artifact caused by errors associated with the small sample size, or prolonged retention of the count indicator particles by the stomach filter. The calculated composition of the diet was, in order of decreasing abundance, *Chironomus zealandicus* (84%), diatoms, macrophyte detritus, *G. pectinatus*, filamentous algae (0.4), the harpacticoid copepod *Braniola canterburyensis* and *P. lucasi*. If the calculated volume of chironomid tissue is excluded from the calculations these proportions (given in the same order) become 0%, 42%, 39%, 4%, 3%, 1.5% and 1%. These values represent the diet of individuals less than 12 mm in length. The suspended food resource was sparse compared with previous months as non-mobile foods had settled to the bottom during a long calm period and *G. pectinatus*, an active swimmer, therefore appears to be relatively more abundant than it was in absolute terms. The suspended food resource was composed of diatoms (42%), macrophyte detritus, filamentous algae, and *G. pectinatus*. The benthic food resource contained a similar quantity of food to the total volume present in February and was composed of diatoms and amphipods in similar proportions, with some macrophyte detritus, harpacticoid copepods, ostracods and filamentous algae. *Chironomus zealandicus* was not considered as a food resource as it appeared to be eaten only by a few of the larger mysids present.

In May the mysids present were between 6 mm and 14 mm in length and no adult females were carrying a brood. The volume of food present in the stomachs of individuals and of the population present declined by factors of 0.4 and 0.2 respectively compared with March (Table 5); this difference was due principally to the absence of chironomid fragments from the mysid stomachs examined. The mysids present ingested a diet composed of equal proportions of diatoms and macrophyte detritus (Fig. 16), *G. pectinatus* (6%), *P. lucasi*, harpacticoid copepods and ostracods. At this time the water column food resource was again small due to calm

conditions, but had increased in overall tissue content by a factor of 1.3 since March. It was composed principally of macrophyte detritus (Table 5). The benthic food resource also showed some reduction in the overall quantity of ingestible tissue present and also consisted mostly of macrophyte detritus. Small quantities of filamentous algae were present.

By June the individuals present ranged from 7-16 mm in length but were not sexually active. These mysids contained only 62% of the mean volume of food per individual, but similar quantities of food as a population compared with the population sampled in May. Their diet was composed of macrophyte detritus, diatoms, equal proportions of filamentous algae and *G. pectinatus*, *P. lucasi*, harpacticoid copepods and ostracods (Table 5). Larger amounts of suspended foods caused a reduction in the relative proportion of *G. pectinatus*, but adult *G. pectinatus* were present at a similar population density to their density in May. The water column food resource was composed mostly of filamentous algae and macrophyte detritus (Fig. 16). The total quantity of tissue present in the benthic food resource was 4.3 times higher than in May at this site and was composed mainly of macrophyte detritus. The observation that *G. pectinatus* was present in the stomachs of mysids in similar proportions in both May and June, despite changes in the availability of other foods, suggests that the different feeding mechanisms used by mysids may not respond to the changing availability of food in the same manner, as selectivity of crustacean filter mechanisms is a constant probability function (Boyd, 1976). This phenomenon was observed at other times.

By July most mysids present were between 9 mm and 15 mm in length. The population sampled individually contained 0.5 times the quantity of food present in the previous month, whereas the ingestion of the population as a whole had fallen by 64% compared with June. The mean volume of food present in each stomach was the least recorded for a mature population of mysids at this site. The diet consisted of macrophyte detritus, diatoms, filamentous algae, *P. lucasi* and *G. pectinatus* (Table 5). There was little suspended material due to calm conditions at the time of sampling. Consequently *G. pectinatus* appears to have increased in significance in the water column food resource but, in fact, it was present in slightly smaller quantities which explains the reduction in the proportion of *G. pectinatus* ingested. The different components of the water column food resource were macrophyte detritus (66%), filamentous algae, *G. pectinatus* (4%), and diatoms. The benthic food resource was 2.9 times as abundant as in June, a change not reflected by changes in the volume of tissue present in the gut and was

composed of filamentous algae (65%), macrophyte detritus, diatoms, harpacticoid copepods, ostracods and smaller quantities of *P. lucasi* (Table 5).

By August the mysid population present consisted of individuals 5-16 mm in length, none of which were breeding. The mean volume of food contained in the stomach of each individual had increased by 25% since July, but the population had ingested 7% less due to declining population densities. The diet was composed of macrophyte detritus, diatoms, filamentous algae and small proportions of *G. pectinatus*, harpacticoid copepods and ostracods (Fig. 16). The total volume of food present in the water column food resource had increased slightly and the resource consisted mainly of macrophyte detritus (Table 5). The benthic food resource contained similar quantities of food to July and also was composed mostly of macrophyte detritus.

No mysids were present at this station in October. Both the water column and benthic food resources contained increased quantities of potential foods, including greater resources of diatoms and some of the benthic animals ingested (Fig. 16). Again, the absence of mysids from this station does not appear to be related to declining supplies of the foods available for ingestion. As several food items are still present in greater quantities than at other sites at which moderate population densities of *T. chiltoni* were present, food quantity does not seem to be limiting distribution at this time.

5.2.2 The Available and Ingested Foods of *Tenagomysis chiltoni* at Site 1

The mysid population present at Site 1 on 26 September 1979 consisted of individuals 9-17 mm in length; adult females were carrying broods. The calculated diet at this time mainly consisted of *Chironomus zealandicus* (71%) (Table 6). *C. zealandicus* fragments were usually associated with large volumes of tissue and sedimentary particles from the chironomids' digestive tracts; similar associations of tissue and sediment were observed also in mysid stomachs which did not have count indicator particles present. Only the larger mysids ingested chironomids. Excluding chironomid tissue, the diet of *T. chiltoni* was composed of macrophyte detritus (43%), diatoms (36%), *G. pectinatus* (8%), filamentous algae (7%) and *Braniola canterburyensis* and *Gomphocythere duffi* (6%) (Table 6). The water column food resource

Table 6. The proportions and changes in volume (multiplication factor) of available and ingested foods of *T. chiltoni* at Site 1.

	Food Type (%)	1979 SEP.	1979 NOV.	1979 DEC.	1980 JAN.	1980 FEB.	1980 MAR.	1980 MAY	1980 JUNE	1980 JULY	1980 AUG.	1980 OCT.
Water column food resource	Diatoms	13	4	10	6	16	5	5	28	4	6	11
	Filamentous algae	12	68	51	55	47	47	13	23	18	9	0
	Macrophyte detritus	74	28	39	39	32	47	80	47	76	85	89
	G. pectinatus	1	0	0	0	5	1	2	2	2	0	0
	Change in volume of food present since previous month	-	1.1	2.3	2.0	0.3	0.4	2.4	0.3	0.2	2.7	2.0
Ingested foods	Diatoms	10	1	3	13	14	27	8	9	3	-	2
	Filamentous algae	2	71	58	34	19	3	13	8	7	-	43
	Macrophyte detritus	14	28	38	53	39	46	62	76	84	-	51
	G. pectinatus	2	0	0	0	27	11	10	6	4	-	0
	Harpacticoid copepods and ostracods	1	0	1	0	0	12	2	1	1	-	0
	P. lucasi	0	0	0	0	0	1	5	0	1	-	4
	C. zealandicus	71	0	0	0	0	0	0	0	0	-	0
	Individual change in volume ingested since previous sample	-	0.2	7.1	0.9	0.5	0.9	3.2	0.6	0.2	-	0.5
	Size range of mysids (mm)	9-17	3-5	2-11	2-11	6-11	7-13	6-14	6-16	6-16	-	10-13
	Population change in volume ingested since previous sample	-	<0.1	3.8	2.8	0.2	0.5	1.1	0.9	0.5	-	0.2
Benthic food resource	Diatoms	24	14	16	35	17	27	3	4	1	7	6
	Filamentous algae	0	2	0	11	4	0	4	0	0	4	6
	Macrophyte detritus	53	9	66	16	47	20	75	54	97	82	77
	Harpacticoid copepods and ostracods	9	1	15	0	2	53	3	6	2	4	0
	P. lucasi	14	74	3	38	30	0	15	36	0	3	11
	Change in volume of food present since previous month	-	1.3	1.8	2.2	0.2	0.6	0.2	1.0	8.8	0.6	1.6

consisted of 74% macrophyte detritus, whereas the benthic food resource was composed of 53% macrophyte detritus, with 24% diatoms. Chironomids have been excluded from calculations of the benthic food resources as most chironomids were not available to mysids because they were within the substrate and many of the mysids present were too small to ingest the available chironomid larvae.

In November members of the population of mysids sampled were 3-5 mm long neuter individuals; the population density and the sampled number of mysids was very low. The individual stomachs examined contained only 0.2 times the volume of tissue and the population had ingested only a small fraction of this proportion compared with the previous month's sample. Most of these differences were attributable to the smaller sizes and lower densities of mysids present. The diet consisted mostly of filamentous algae. No animal tissue was ingested. The water column food resource contained higher concentrations of tissue, principally filamentous algae, than in September and very small quantities of *Gladioferens pectinatus* tissue. The benthic food resource had also increased and contained mainly amphipods.

In December the mysid population was still at a low density at this site; individuals measured 2-11 mm in length and were, with one exception, all neuter. Individual stomachs contained seven times as much food as in November and the population ingested 3.8 times the volume of food compared with the same site in November, whereas the benthic food resource contained 1.8 times the concentration of materials. The water column food resource was composed mostly of filamentous algae and macrophyte detritus. The benthic food resource was comprised mainly of an unsampled quantity of filamentous algae and macrophyte detritus.

In January the mysids present ranged from 2 mm to 11 mm in length and no adult females carried a brood. The mean volume of food present in the stomach of each mysid was slightly lower than in December, but the population present had ingested about three times as much food as in December. The mysids' diet consisted of macrophyte detritus, filamentous algae, diatoms and insignificant proportions of animal tissues. Twice the volume of potential food was present in the water column food resource compared with December; it consisted mostly of filamentous algae and macrophyte detritus. Over twice the volume of potential food was present in the benthic food resource which consisted mainly of diatoms and the amphipod *Paracorophium lucasi*. The volume of *P. lucasi* tissue ingested by

these *Tenagomysis chiltoni* was negligible compared with the abundance of the amphipod in the food resource.

Individuals within the mysid population sampled in February ranged from 6 mm to 11 mm in length and were not reproducing. Individuals contained only half the volume of food present in January and the population only ingested about 20% of the volume of food consumed in January. The diet was composed of macrophyte detritus, *G. pectinatus*, filamentous algae, diatoms and small volumes of animal tissue other than *G. pectinatus* (Table 6). Small amounts of food were present within the suspended food resource, mainly filamentous algae and macrophyte detritus. The ingestion of *G. pectinatus* was out of proportion to its abundance in the water column resource. The concentration of food available within the benthic food resource was less than in January and was composed mostly of macrophyte detritus and *P. lucasi*. *Gomphocythere duffi* contributed 2% of this resource but was not ingested.

By March most of the mysid population present were individuals 7-13 mm in length. The population had by now ceased to breed until spring. Mysid stomachs contained slightly less food per individual and half the volume of food as a population than in February (Table 6). The mysids had ingested macrophyte detritus, diatoms, harpacticoid copepods and ostracods (12%), *Gladioferens pectinatus* (11%), filamentous algae (3%) and amphipods (1%). The suspended fraction of the water column food resource (the diatoms, algal filaments and macrophyte detritus) contributed less volume than in February to a resource depleted by the higher density immobile components settling out during calmer weather. The resource was composed mostly of equivalent proportions of filamentous algae and macrophyte detritus. The benthic resource contained less potential food than in February, mainly *Braniola canterburyensis*, diatoms and macrophyte detritus. *B. canterburyensis* formed 87% of the large quantity of harpacticoid copepod and ostracod tissue ingested. This maximum peak in the proportion of diatoms consumed by the mysid coincides with the second greatest relative and absolute abundance of diatoms within the benthic resource at this site.

Individuals within the mysid population at Site 1 in May were from 6 mm to 14 mm long. Individual stomachs contained about three times more food than in March, whereas the population contained similar quantities of food compared with March. The apparent rise in ingestion rate may have been produced partly by a decreasing rate of ingestion due to rapidly falling water temperature. The diet was composed mostly of macrophyte

detritus, although *G. pectinatus* formed 10%, *P. lucasi* 5% and the harpacticoid copepods (*B. canterburyensis* and *Tachidius* sp.) 2%. The water column food resource contained 2.4 times more potential food than in March and the resource consisted mainly of macrophyte detritus. The benthic food resource was markedly depleted compared with March and contained mostly macrophyte detritus, with amphipods forming 15%. The change in the volume consumed by an individual was not related to changes in the length structure of the population present and occurred in an opposite manner to the change observed in the abundance of the benthic food resource.

By June the mysids present were 6-16 mm in length. As a population the stomachs contained similar quantities to May but less as individuals. Their diets were composed principally of macrophyte detritus. Calm conditions were again encountered at the time of sampling which, combined with small numbers of *G. pectinatus*, contributed to the continued low levels of ingestible tissue within the water column food resource. The resource contained macrophyte detritus, diatoms, filamentous algae and *G. pectinatus*. The benthic food resource contained a very similar overall concentration of edible tissue to that present in May and was composed mostly of macrophyte detritus and amphipods with harpacticoid copepods, including *Tachidius* sp. which was not ingested. While the overall abundance of *P. lucasi* had increased since May the proportion ingested fell to negligible amounts. This lack of relationship between availability and ingestion of *P. lucasi* was observed frequently.

In July mysids between the lengths of 6mm and 16 mm were present. The volume of food present within their stomachs was calculated to be half that present in June with individual stomachs on average 0.2 times less than in June. The mysids had ingested mostly macrophyte detritus. The concentration of potential foods within the water column had decreased markedly since the June sampling period and the composition was mainly macrophyte detritus. The benthic food resource was calculated to have increased ninefold and consisted almost entirely of macrophyte detritus.

No mysids were present at this site in August. The water column food resource, again mainly macrophyte detritus, contained 2.7 times more food material than in July. The benthic food supply was similar in composition to that present in July, except that the supply of macrophyte detritus had been reduced to more normal winter concentrations. The greater relative abundance of macrophyte detritus in the food resources over winter correlated with the increased consumption of macrophyte in this season.

In October only 13 mysids were captured at this station; these measured 10 mm to 13 mm in length. The stomach of each contained on average 47% of the volume of food contained in July at this site, but the water temperature had increased by 10°C during the intervening period, which would influence the gut velocity (Elliot and Persson, 1978). The diet consisted principally of macrophyte detritus and filamentous algae. The water column food resource contained twice the volume of ingestible tissue it contained in August and thus approached the available food concentration observed in July. This resource was still composed mostly of macrophyte detritus. The benthic food resource had increased and contained increased proportions of amphipods (11%) but was composed principally of macrophyte detritus.

5.2.3 The Available and Ingested Foods of *Tenagomysis chiltoni* at Site 2

In September 1979 the overwintered mysids present at Site 2 were 8-15 mm in length; no adult females carried a brood. The population as a whole consumed mostly macrophyte detritus, diatoms and filamentous algae (Table 7). Foods available in the water column were mainly filamentous algae and macrophyte detritus, whereas the benthic foods available were mainly macrophyte detritus, diatoms and *Paracorophium lucasi*.

By November most of the mysids present were only 3-8 mm in length and were neuter individuals belonging to the spring generation; five mysids present were all adult females carrying broods and were residual members of the overwintered stock. Despite the decrease in the modal size of mysids, the average ingested volume was similar to that observed during September due to a higher population density, presence of the large adult females and the greater volumes of food which they consumed and also the greater food resources present. The population contained 53% more food as a result of increased population densities. The diet was contributed to principally by filamentous algae and macrophyte detritus. All the animal tissues ingested were consumed by the larger overwintered mysids (*Gladioferens pectinatus* and small amounts of *P. lucasi* tissue). The water column food resource had increased 2.8 times and also consisted mainly of filamentous algae and macrophyte detritus. The benthic food resource had enlarged by a slightly smaller factor and contained mainly amphipods and diatoms. Very small quantities of amphipod tissue were ingested despite its relative abundance at this site. Moderate quantities of filamentous algae were present but not represented in substrate samples.

Table 7. The proportions and changes in volume (multiplication factor) of available and ingested foods of *T. chiltoni* at Site 2.

	Food Type (%)	1979 SEP.	1979 NOV.	1979 DEC.	1980 JAN.	1980 FEB.	1980 MAR.	1980 MAY	1980 JUNE	1980 JULY	1980 AUG.	1980 OCT.
Water column food resource	Diatoms	6	16	8	11	4	6	11	6	13	5	9
	Filamentous algae	58	44	63	38	36	49	48	29	12	6	2
	Macrophyte detritus	36	39	29	48	55	42	39	62	74	87	88
	G. pectinatus	0	1	0	3	5	3	2	3	1	2	1
	Change in volume of food present since previous month	-	2.8	1.0	1.8	1.1	0.4	1.3	0.4	1.4	4.3	1.6
Ingested foods	Diatoms	30	19	19	11	12	17	6	7	3	4	8
	Filamentous algae	22	42	36	35	17	13	16	15	7	8	9
	Macrophyte detritus	48	34	44	46	51	54	66	68	70	64	57
	G. pectinatus	0	5	1	5	19	9	8	9	8	19	6
	Harpacticoid copepods and ostracods	3	0	0	0	0	2	0	0	4	2	11
	P. lucasi	7	0	0	3	1	5	4	1	8	3	5
	C. zealandicus	0	0	0	0	0	0	0	0	0	0	4
	Individual change in volume ingested since previous sample	-	0.9	7.1	0.4	0.9	0.5	1.9	0.7	1.5	0.6	0.7
	Size range of mysids (mm)	8-15	3-8	5-10	3-12	3-15	7-14	7-15	7-16	6-15	5-16	8-15
	Population change in volume ingested since previous sample	-	1.5	12.8	0.9	0.5	0.2	0.7	1.0	1.1	0.4	0.5
Benthic food resource	Diatoms	28	40	23	31	12	22	6	5	2	2	5
	Filamentous algae	9	0	0	0	0	6	1	0	2	0	0
	Macrophyte detritus	37	13	74	13	49	60	49	73	95	96	88
	Harpacticoid copepods and ostracods	2	2	3	2	0	1	1	3	1	0	3
	P. lucasi	29	45	0	54	38	11	43	19	0	2	4
	Change in volume of food present since previous month	-	1.7	2.7	1.2	2.2	0.5	3.0	1.7	1.7	0.1	0.2

In December mysids ranged from 5 mm to 10 mm in length and were all members of the spring generation; while adult males were present, no females were breeding. Compared with November the individuals present contained over seven times the volume of food and only a small fraction of this increase was a result of growth of the mysids. The population density had almost doubled during this time. The ingested foods were mostly macrophyte detritus and filamentous algae. The water column foods available consisted mostly of filamentous algae. The benthic food resource had increased by a factor of 2.7; it contained mostly macrophyte detritus. *Braniola canterburyensis* and *Gomphocythere duffi* were present but not consumed (Table 7). While *G. duffi* was not ingested in quantity at several sites at which it was abundant, it was unusual that *B. canterburyensis* was not taken at times when it occurred within the benthic food resource. The low ingestion of animal tissues generally was probably a reflection of the low levels of animal tissues in both food resources and thus not associated with the seasonal successions of the mysid population.

The population sampled in January consisted of individuals 3-12 mm in length, most of which were over 6 mm long. The mean quantity of food present in the stomachs of *T. chiltoni* individuals fell markedly, but that of the population only slightly. The mysids again consumed mostly macrophyte detritus and filamentous algae. The volume of the water column food resource had almost doubled, possibly as a result of wave action, and also consisted mainly of macrophyte detritus and filamentous algae. The benthic food concentration had increased 1.2 times and over half consisted of the amphipod *P. lucasi*. This change was not reflected in the diet of *T. chiltoni*. The reduction in the quantity of food ingested by each individual appeared to be related to the turbulence of the water created by the wave action as at some other sites.

In February the mysids sampled were 3-15 mm in length and most individuals were over 7 mm in length. All adult females present carried broods. The population ingested half the volume of food compared to January. The diet of mysids present at Site 2 consisted mostly of macrophyte detritus but *Gladioferens pectinatus* contributed 19%, the greatest proportion of the mysids' diet recorded at this site during this study. The water column food supply was slightly more abundant in the previous month and contained mainly macrophyte detritus and filamentous algae, but also contained a small proportion of *G. pectinatus*. The benthic food resource was approximately twice as abundant and contained macrophyte

detritus, *P. lucasi* and diatoms. Moderate waves were induced by winds of force 3-4 on the Beaufort Scale.

By March most of the population at this site were larger (7-14 mm in length) and some adult females were breeding. The volumes of food contained in the stomachs of individuals and the population as a whole were 0.5 and 0.2 times the volume present the previous month respectively (Table 7). The main component of the diet was macrophyte detritus. The water column foods were less abundant, probably due to the prevailing flat calm, and principal potential foods present were filamentous algae and macrophyte detritus. The benthic food resource was half the overall abundance observed in February and was composed mostly of macrophyte detritus. The decline in the quantity of food ingested probably resulted from a decline in the food supply as waves were only 20 cm high and are unlikely to have influenced ingestion.

In May the mysids present were within a similar size range (7-15 mm in length) and sexually inactive. Individual stomachs contained about twice, and the whole population 0.7 times, the food volume present in March. The principal component of the diet was macrophyte detritus. The water column food resource contained slightly more potential food material which consisted mostly of filamentous algae and macrophyte detritus. The potential benthic foods present were three times more abundant than a month previously and contained mainly macrophyte detritus and *P. lucasi*. A relatively small proportion of amphipods were consumed in comparison with abundance in the benthic food resource.

By June individuals within the mysid population were between 7mm and 16 mm in length. The stomachs of the population contained similar quantities of food to the May population; individual stomachs contained 0.7 times the volume of food. As water temperatures were falling between the two sampling times, these figures are not strictly representative of ingested volumes of food. The observed diet consisted mostly of macrophyte detritus. The water column food resource was much less than in May whereas benthic foods were more abundant.

In July the mysids present measured 6-15 mm in length. The population ingested about the same quantity of food as in June but individuals ingested about 1.5 times more food. The main item of diet was macrophyte detritus. Suspended foods were half as abundant as in the previous month. Benthic foods were present at an overall concentration of 1.7 times that found in June and consisted predominantly of macrophyte detritus.

In August the population of mysids was formed by individuals 5-16 mm in length. The population and individuals within the population ingested less than in July (Table 7). The mysids present consumed mostly macrophyte detritus with *G. pectinatus* contributing 19%. The water column foods were over four times more abundant than in July, probably due to moderate wave action suspending benthic materials. The resource also contained mostly macrophyte detritus. The benthic foods were one-tenth the volume calculated for July and consisted almost entirely of macrophyte detritus. An unusually large proportion of *G. pectinatus* was ingested in view of its low concentration and relative abundance within the food resource.

Site 2 was the only sampling station at which a full sample was collected in October. The members of the mysid population sampled were between 8 mm and 15 mm in length and brood-carrying adult females were present at this station for the first time since March. The stomachs of members of the population contained half the volume of food present in August, whereas individual stomachs contained 0.7 times the volume of food. These values are not as indicative of the relative volumes ingested as the water temperature had risen 8°C since August. The mysids present consumed mostly macrophyte detritus but a relatively high proportion (11%) of harpacticoid copepods. The water column contained 1.6 times the quantity of food present in August, which was partly as a consequence of moderate to heavy wave action at this site; the benthic food resource was markedly depleted. Both resources consisted mostly of macrophyte detritus.

5.2.4 The Available and Ingested Foods of *Tenagomysis chiltoni* at Site 3

In September 1979 the overwintered generation present at Site 3 were 9-16 mm in length and were actively reproducing. Their diet consisted mostly of macrophyte detritus (Table 8). The water column food resources mainly consisted of macrophyte detritus, filamentous algae and diatoms, whereas the benthic foods present were *Paracorophium lucasi*, diatoms and macrophyte detritus. *P. lucasi* were not ingested in quantities proportional to the prey species abundance within the lake.

By November there were more smaller mysids, those sampled were 5-15 mm in length and were larger (on average) than mysids present at other sites at this time. The individual mysids ingested 2.6 times more food than in September at this site, and the population consumed over three times more

food (Table 8). The diet was composed of macrophyte detritus, diatoms and filamentous algae with some *G. pectinatus* (10%) and small amounts of *P. lucasi*. The volume of food in the water column had increased, despite calm conditions, and consisted mostly of filamentous algae together with diatoms and macrophyte detritus. The benthic food resource had increased threefold and was composed mainly of diatoms (72%). Algal mats were present on top of the substrate.

In December most mysids present were between 10 mm and 16 mm in length and the population contained many breeding females from the over-wintered population. The mysids present contained 21 times more food than the population in November, whereas individuals contained 7 times more food. The mysids present had eaten predominantly macrophyte detritus and filamentous algae (Table 8). The water column food resource contained nearly three times more food material than in November although calm conditions again prevailed and the main component was filamentous algae (72%) with less macrophyte detritus (19%). Benthic foods were less abundant than in November with macrophyte detritus (69%) and diatoms only 29%. The unusually large discrepancies between the availability and utilisation of filamentous algae and macrophyte detritus may represent sampling error, caused by disturbance of algal mats growing on the substrate.

In January non-reproductive mysids 2-11 mm in length were present and most mysids were over 9 mm long. The population of mysids ingested less food than in December; individuals ingested 0.2 times the volume of food. The diet consisted mostly of macrophyte detritus with less diatoms and filamentous algae and only 11% *G. pectinatus* and 1% *P. lucasi*. The water column food resource was 2.7 times more concentrated than in December, due principally to moderately heavy wave action. The resource contained principally macrophyte detritus, filamentous algae and diatoms. The benthic food resource was three times more concentrated than in December and consisted mainly of amphipods, diatoms and macrophyte detritus. As the mean ingestion per individual was reduced to one-fifth, whereas both food resources tripled compared with December, it appeared that moderate to heavy wave action may inhibit feeding activity or make feeding activity difficult either directly or through the suspension of heavy sediment loads; similar observations were made on other occasions. *T. chiltoni* is absent from the littoral zone in heavy surf suggesting that the mysid avoids turbulent waters.

Table 8. The proportions and changes in volume (multiplication factor) of available and ingested foods of *T. chiltoni* at Site 3.

	Food Type (%)	1979 SEP.	NOV.	DEC.	1980 JAN.	FEB.	MAR.	MAY	JUNE	JULY	AUG.	OCT.
Water column food resource	Diatoms	24	26	8	22	21	14	39	30	3	13	17
	Filamentous algae	34	50	72	31	19	8	21	51	35	11	38
	Macrophyte detritus	40	23	19	45	54	67	38	18	59	76	43
	G. pectinatus	2	1	1	2	6	11	2	1	3	0	2
	Change in volume of food present since previous month	-	1.6	2.9	2.7	0.3	1.8	3.8	1.4	0.6	2.7	0.3
Ingested foods	Diatoms	8	28	5	22	6	3	5	3	1	1	11
	Filamentous algae	7	26	39	20	13	3	23	20	8	20	1
	Macrophyte detritus	80	36	56	46	48	20	56	73	74	78	78
	G. pectinatus	2	10	1	11	30	73	16	2	12	0	1
	Harpacticoid copepods and ostracods	1	0	0	0	1	0	0	2	4	1	9
	P. lucasi	2	0	0	1	2	1	0	0	0	0	0
	C. zealandicus	0	0	0	0	0	0	0	0	0	0	0
	Individual change in volume ingested since previous sample	-	2.6	6.9	0.2	2.0	0.2	2.2	0.7	1.6	1.5	0.4
	Size range of mysids (mm)	9-16	5-15	10-16	2-11	9-13	7-12	6-14	5-14	5-16	12-17	8-16
	Population change in volume ingested since previous sample	-	3.1	21.0	0.4	0.9	0.1	1.1	1.1	0.9	0.9	0.9
Benthic food resource	Diatoms	33	72	29	36	11	8	3	5	2	2	7
	Filamentous algae	0	0	0	0	0	0	0	0	27	1	0
	Macrophyte detritus	26	17	69	27	76	80	83	69	68	97	71
	Harpacticoid copepods and ostracods	0	11	0	3	2	1	3	2	3	0	11
	P. lucasi	41	0	2	44	11	11	11	24	0	0	11
	Change in volume of food present since previous month	-	3.0	0.6	3.0	0.3	1.0	1.9	0.9	0.4	4.2	0.2

By February most of the mysid population at Site 3 was 9-13 mm in length and all adult females had developing larvae in the marsupium. The population ingested almost the same quantity of food as it had ingested in January, due to declining population density. Individuals ingested twice the volume of food. As the quantity of both the water column and benthic foods fell, the factor previously exerting an adverse influence upon feeding must have been no longer operative. The lake was calm again; light penetration, dissolved oxygen and water temperature were similar to January while salinity had increased progressively from December to February and is therefore unlikely to have caused a reduction in the intensity of feeding. The mysids ingested mainly macrophyte detritus and *G. pectinatus*. Animal tissues comprised 33% of the diet of this breeding population. The food availability within the water column decreased 3-4 times. The principal potential food item was macrophyte detritus with *G. pectinatus* only 5%. The overall quantity of available food in the benthic resource fell slightly and also consisted mostly of macrophyte detritus. The changes since the previous month in the composition of either food resource resembled changes in the diet, and marked selectivity of *G. pectinatus* from the water column had occurred (as has frequently appeared to be the case at other times in this study). Very little benthic food had been ingested and mysid stomachs containing benthic food also contained water column foods.

In March most mysids were 7-12 mm in length and all adult females were breeding. The population contained 0.2 times the volume of food. The lake was calm. Mysids ingested mostly *G. pectinatus* and less macrophyte detritus and filamentous algae. The concentration of food within the water column increased; its constituents were mainly macrophyte detritus with *G. pectinatus* forming 11%. The overall amount and composition of the benthic food resource was almost identical to February with the resource composed mostly of macrophyte detritus. The proportion of *G. pectinatus* ingested was 6.6 times greater than the fraction this copepod formed of the suspended foods available. The abundance of *G. pectinatus* and the contribution it made to the diet of *T. chiltoni* were at their maximum values recorded during this study, a month later than the maximum salinity recorded (14.7%).

Over the last three months, as the proportion of the diet composed of animal tissues increased, the proportion of living plant material ingested by the mysids declined. This change appears to be related to the relative abundance of various food materials. However, the nature of both the water column and benthic resources is too variable to exclude selectivity effects.

The volume of *G. pectinatus* ingested was probably at its maximum in February as a larger volume of tissue was present in the stomach and higher water temperatures probably decreased gut passage times. This observation coincides with the maximum absolute abundance of *G. pectinatus* observed in the field.

By May individuals of the mysid population measured 6-14 mm in length and had ceased to breed. Individual stomachs contained 2.2 times more food than in March but the population contained about the same amount of food. The mysids ingested principally macrophyte detritus and only 16% *G. pectinatus* and small quantities of other animal tissues. The water column food resource contained almost four times the concentration of food it contained in March, particularly diatoms, macrophyte detritus and filamentous algae (Table 8). The benthic foods were almost twice as abundant as in March and consisted mostly of macrophyte detritus. *Gomphocythere duffi* and *P. lucasi* were present but not ingested, or ingested in minimal quantities, despite relative abundances of 3% and 11% respectively. The lack of ingestion of these species at times when they occurred with moderate frequency was observed on other occasions.

In June mysids 5-14 mm in length were present at Site 3. The stomachs of individuals contained 0.7 times the volume of food in May, whereas the population contained 1.1 times the amount of food. The diet was mainly macrophyte detritus and (less) filamentous algae. Water column foods were more abundant than in May and were composed mostly of filamentous algae with less macrophyte detritus. The benthic foods were similar in quantity to May and consisted mostly of macrophyte detritus and *P. lucasi*. *G. duffi* (contributing 2%) was only ingested in very small quantities. Water temperatures at this site were similar in this and the succeeding two months.

In July mysids present measured 5-16 mm in length. Individually these ingested more food than in June whereas as a population the mysids consumed about the same volume of food as in June. Their diet was composed mostly of macrophyte detritus (Table 8) with 12% *Gladioferens pectinatus*. The food resource within the water column was less than in June and was composed principally of macrophyte detritus and algal filaments with *G. pectinatus* 3%. The benthic food resource was less than in June and mainly macrophyte detritus and algal filaments. The consumption of harpacticoid copepods was much higher relative to their density within the food resource than was the consumption of *Gomphocythere duffi*.

Only five mysids were collected at this site in August and these were between 12 mm and 17 mm in length. Each mysid had ingested about 1.5 times more food than in July; apparently lack of feeding success was not therefore limiting the distribution of *T. chiltoni*. The population as a whole only ingested 0.9 times the quantity of food ingested in July due to the low population density. The diet was composed mostly of macrophyte detritus and some filamentous algae. The water column and benthic food resources had increased in abundance by factors of 2.7 and 3.2 respectively. Macrophyte detritus was most common in both food resources. Minimal quantities of *Braniola canterburyensis* were present in the substrate sampled.

Only 15 mysids 8-16 mm in length were found at Site 3 in October. These were reproductively active. They ingested only 0.4 times the quantity of food ingested by each mysid in August whereas as a population 0.9 times the quantity of food was ingested. Their diet consisted mostly of macrophyte detritus. The water column food resource was only 0.3 times as abundant as in August despite moderate wave action and was composed mostly of macrophyte detritus and filamentous algae (Table 8). The benthic food resource was 0.2 times the concentration present in August. It contained principally macrophyte detritus but harpacticoid copepods and Amphipoda each contributed 11%.

The small size of the mysid samples collected during August and October would, as on several other occasions, increase the influence of random errors, on the observed diet. This variability is caused by size-specific differences in the diets of mysids in a similar food resource and variation of each individual's experience of heterogenous distributions of food particles within the water column and benthic food resources within a mysid's vicinity, amongst other factors. Less importance should therefore be attached to the results from this site in the last two months of this study.

As a summary of the complex variations observed in the composition of diet and fluctuations in the availability of foods in the vicinity of a mysid, Figures 16, 17, 18 and 19 are appended to this section.

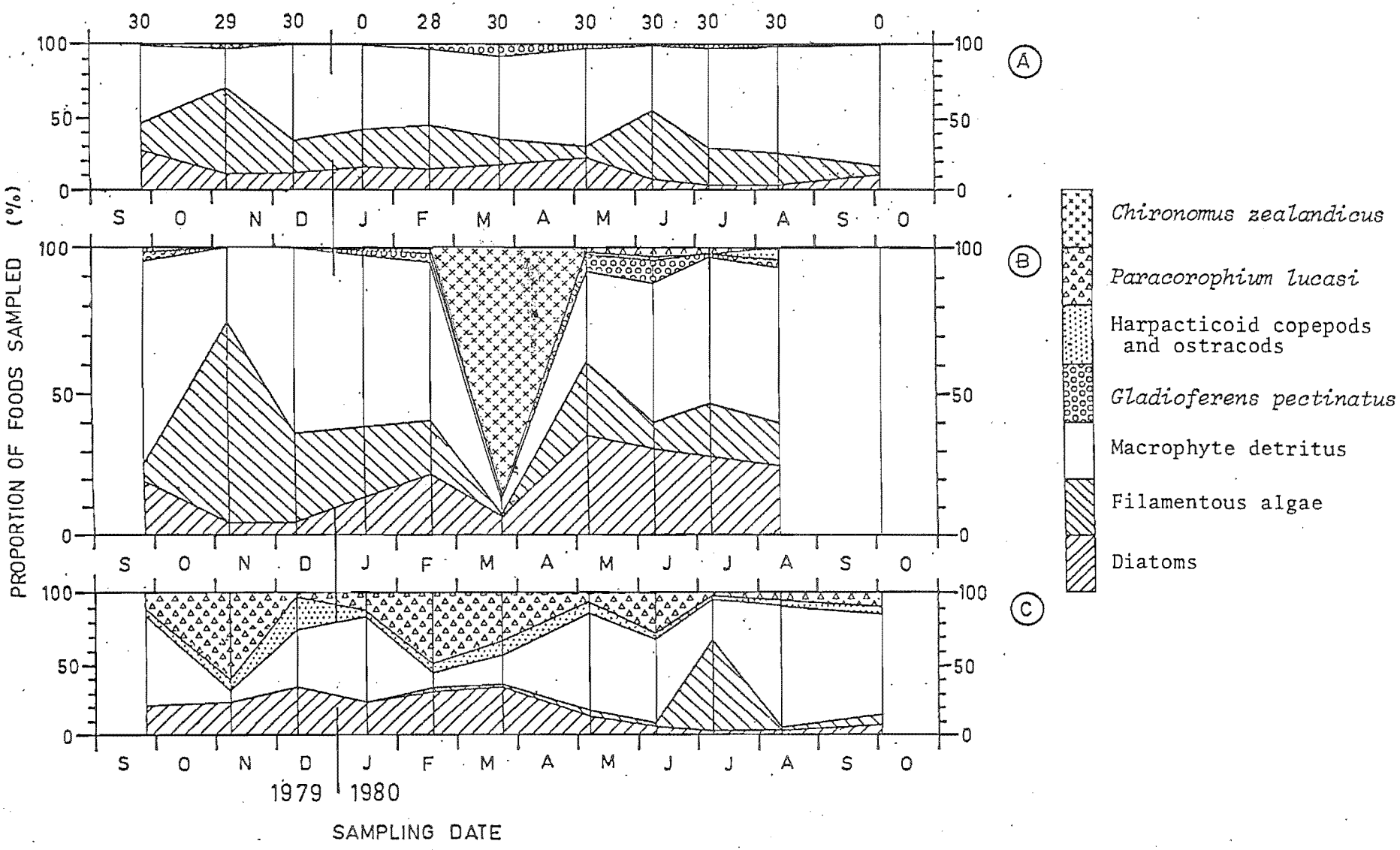

Fig. 16 The available and ingested foods of *Tenagomysis chiltoni* at Site M. Graph A shows the proportions of water column food resources; Graph B shows the proportions of foods ingested by *T. chiltoni*; Graph C shows the proportions of benthic food resources. The number of specimens of mysids examined in each sampling period is given at the top of the three graphs.

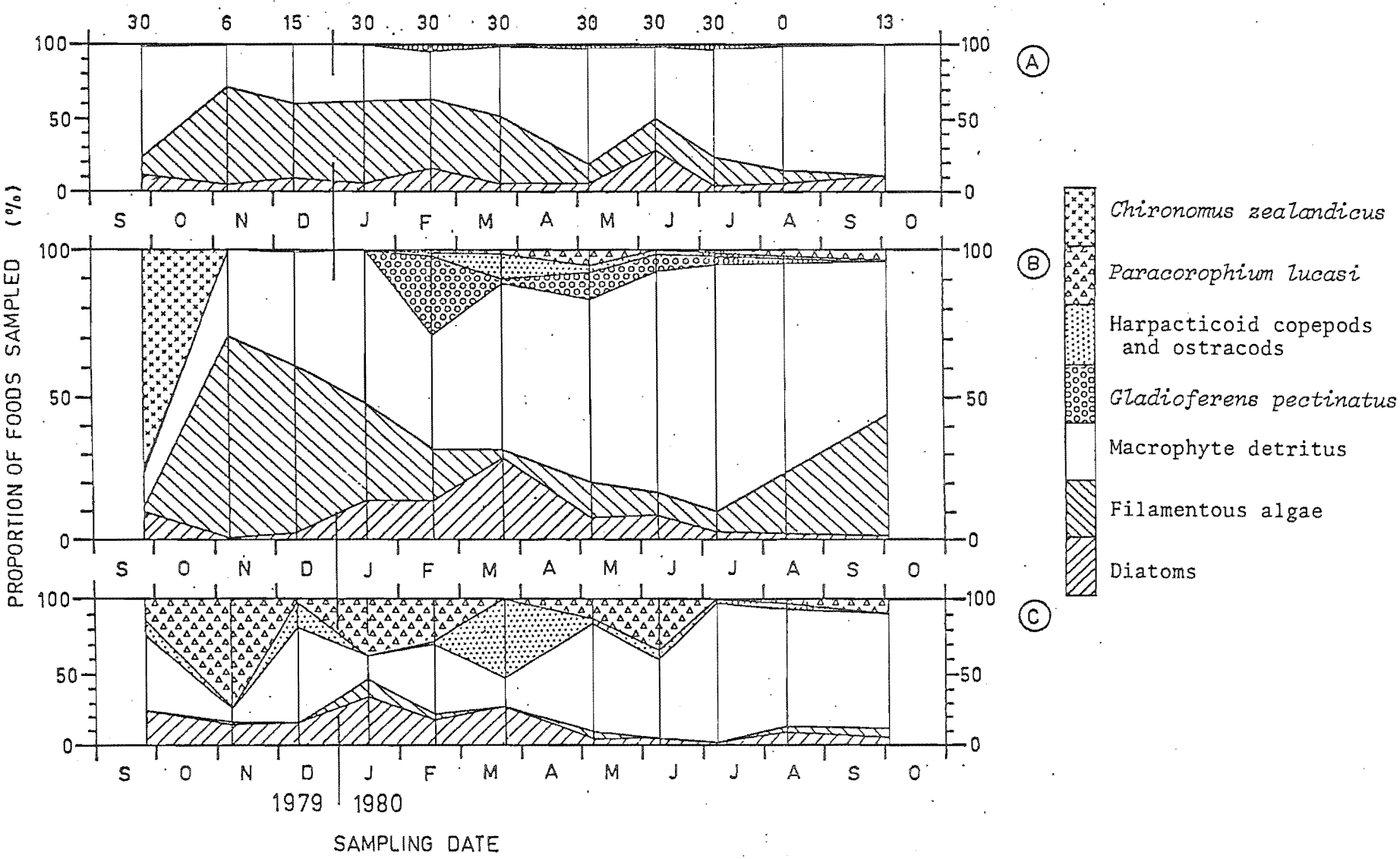

Fig. 17 The available and ingested foods of *Tenagomysis chiltoni* at Site 1. Graph A shows the proportions of water column food resources; Graph B shows the proportions of foods ingested by *T. chiltoni*; Graph C shows the proportions of benthic food resources. The number of specimens of mysids examined in each sampling period is given at the top of the three graphs.

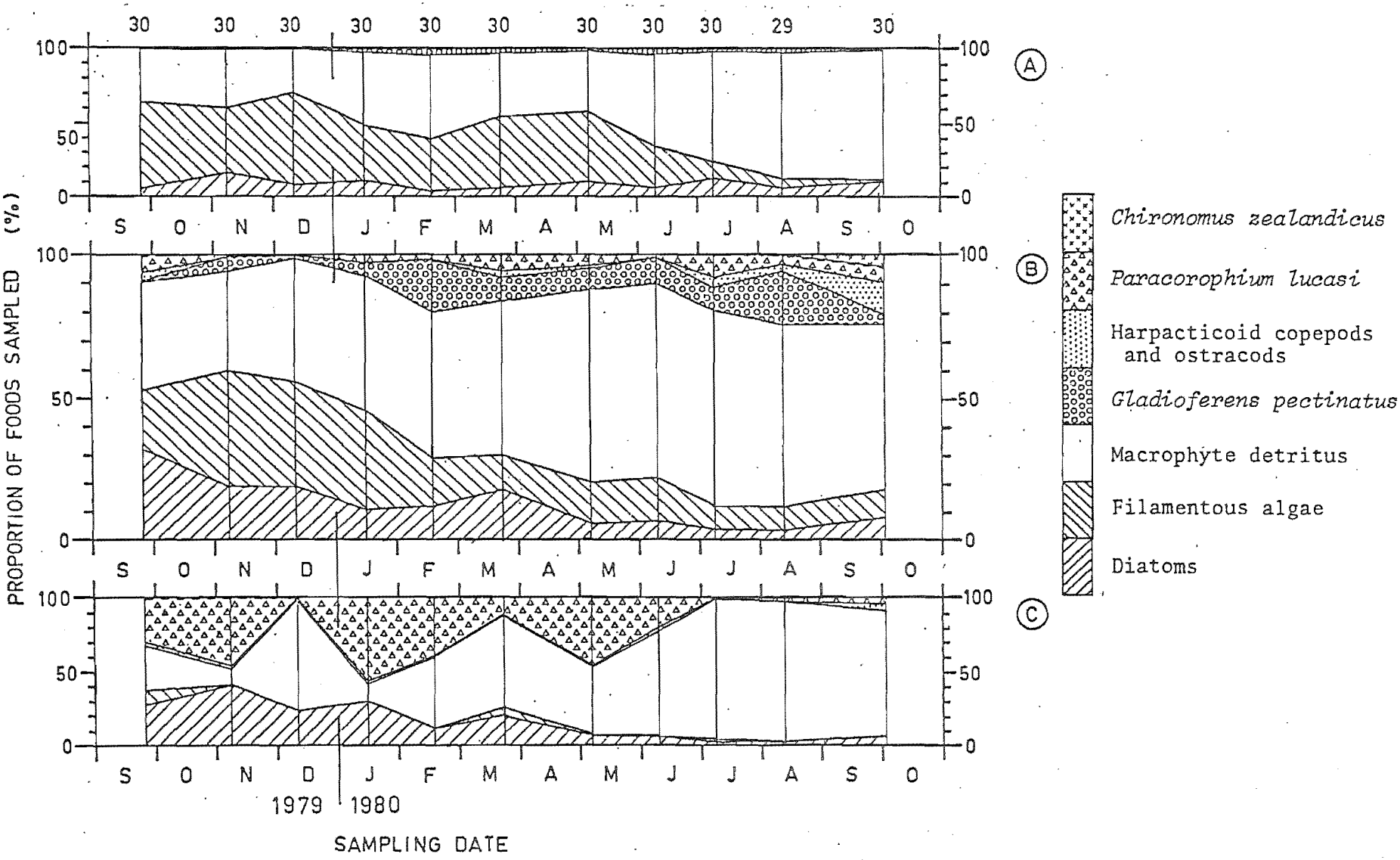

Fig. 18 The available and ingested foods of *Tenagomysis chiltoni* at Site 2. Graph A shows the proportions of water column food resources; Graph B shows the proportions of foods ingested by *T. chiltoni*; Graph C shows the proportions of benthic food resources. The number of specimens of mysids examined in each sampling period is given at the top of the three graphs.

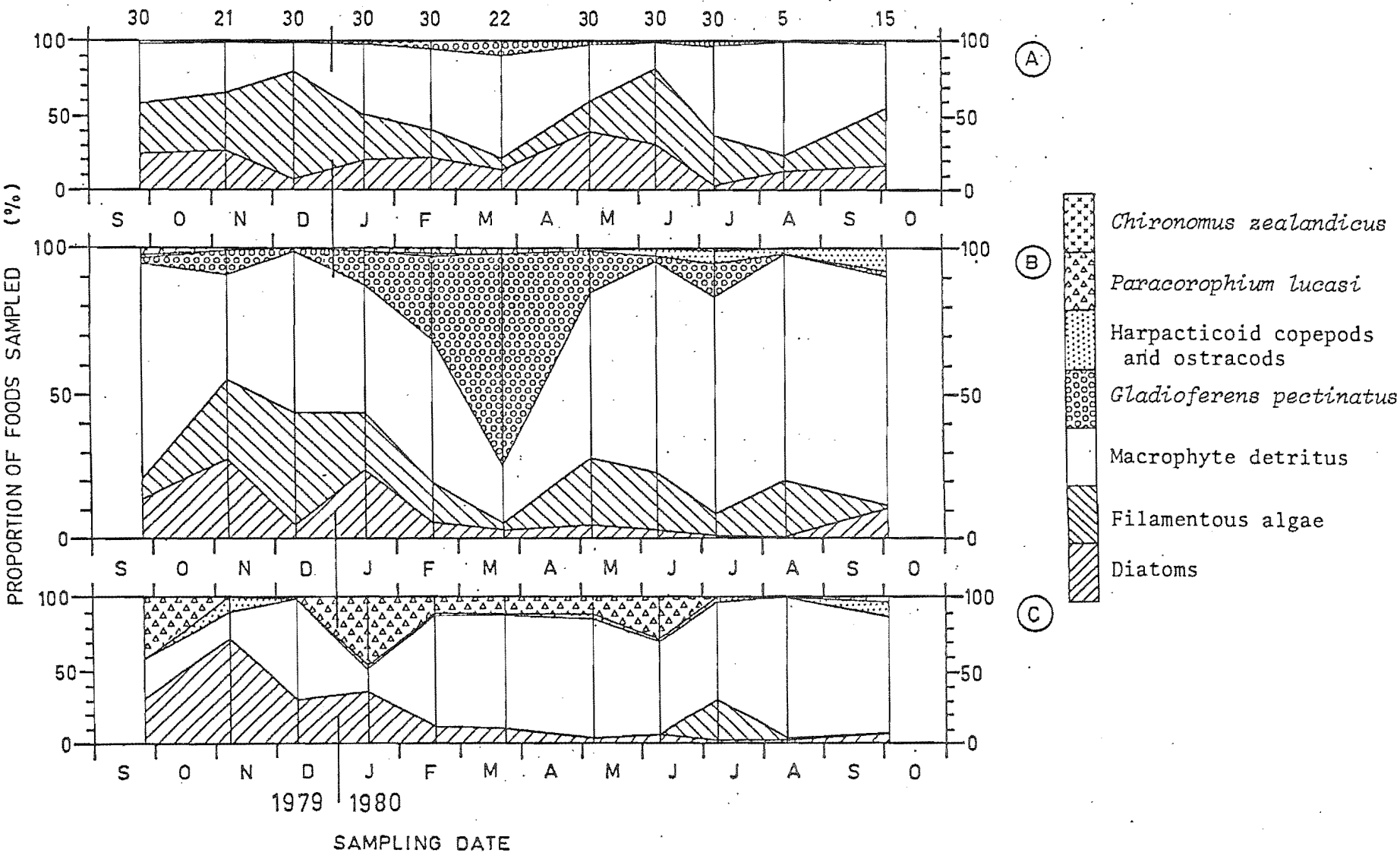

Fig. 19 The available and ingested foods of *Tenagomysis chiltoni* at Site 3. Graph A shows the proportions of water column food resources; Graph B shows the proportions of foods ingested by *T. chiltoni*; Graph C shows the proportions of benthic food resources. The number of specimens of mysids examined in each sampling period is given at the top of the three graphs.

5.3 DISCUSSION

5.3.1 The Influence of Change in Population Structure Upon Diet

It has been shown several times during this study that the characteristics of an individual influence dietary selection by *Tenagomysis chiltoni*. The influence of these factors is not normally visible in natural populations as the observed diet is a composite product of the varying reactions of the individuals comprising the population, related to their nutritional and developmental status. In this study developmental changes occurred in a population; on several occasions changes in the diet were noted. At all four sites the appearance of large numbers of post-larvae in November and December was accompanied by a reduction in both the quantity and relative amount of animal tissues consumed by the population present in December even when the abundance of the animal prey resource available had increased. When animal tissues were consumed in November, the consumer was invariably a member of the larger overwintered population. At Site 2 where both small spring generation and larger overwintered members of the population occurred, with access to the same range of foods, the overwintered mysids present accounted for all the ingested *Gladioferens pectinatus* and *Paracorophium lucasi* tissue. This clearly demonstrates the influence of stage of development on the diet observed in natural populations of *T. chiltoni*; thus the whole life-cycle of an organism must be studied in dietary investigations (Pyke *et al.*, 1977).

Smaller mysids ingest larger proportions of plant material than larger, more predatory mysids (Chapter 4). The increased proportion of filamentous algae ingested in November therefore appears to be partly a result of the increased absolute abundance and relative abundance (excepting Site 2), of filamentous algae within the water column at all sites, and partly a consequence of ontogenetic changes within the mysid population. Determinations of the abundance of filamentous algae within the benthic food resource are unreliable. Changes in the proportions of detritus and diatoms ingested, in relation to the observed changes in population structure, are less consistent in their relation to the food resource than changes in the ingestion of filamentous algae, suggesting that filamentous algae are more easily handled by the mysids than other foods available. Smaller mysids ingested less heavily silicified diatoms; it is therefore possible that the calculation of the quantities of diatoms within the food resources which were available to small mysids was overestimated. Macrophyte detritus may be partially displaced from the diet by large increases in the quantities of filamentous algae available.

Between December and February as the mysid grows, increasing proportions of animal tissues of all types are ingested (Figs 16, 17, 18 and 19) and these include the largest common prey species, the amphipod *Paracorophium lucasi*, in increasing concentrations at most sites. These changes are not always closely related to changes in the availability of prey within the food resource. As the spring generation developed it ingested increasing proportions of the benthic animal food resource, not normally in relation to the estimated abundance of harpacticoid copepods, ostracods or amphipods within that food resource. Larger mysids have access to a greater quantity and improved quality of food within the lake.

Individual variation in ingestion by *T. chiltoni* was present at other times, but masked by the less diverse structure of the mysid population present. The influence exerted by stage of development upon diet shows seasonal variation in shrimps from several different orders (Hanson and Goodwin, 1977; Kost and Knight, 1975; Ross, 1981; Śmiles and Pearcy, 1971; Siegfried and Kopache, 1980) and other crustacea (Chapman and Lewis, 1976; Hill, 1976).

5.3.2 The Influence of Environmental Parameters on Diet

The mean volume of food present in a stomach also appeared to be influenced by the turbulence of the water column. As wave action increased, the concentration of food particles within the water column increased and in these conditions the mysid had noticeably more food present in its stomach than during calm conditions. However, as wave height increased to over 40 cm, the volume of food present per stomach decreased by as much as ten times, compared with mysids in comparable but sheltered stations. Depression of the feeding of littoral organisms due to wave action has been recorded for starfish (Menge, 1972). As wave action increased further *T. chiltoni* moved out of the littoral zone, as has been observed in other mysids (Borodich and Havlena, 1973). The amount of wave action occurring exerted a greater influence on changes in the concentration of food material within the water column between months than did seasonal variations in the supply of the resources available. An important relationship therefore exists between the concentration of some foods within the water column resource, and the benthic resource from which these food particles are suspended by wave-induced currents.

The effects of variations in other environmental parameters are not obvious. The highest salinities and water temperatures observed in the

lake coincide closely with the ingestion of larger volumes of animal tissues, particularly of the copepod *Gladioferens pectinatus* which lives in the water column. However, the increase in the ingestion of *G. pectinatus* is more strongly associated with the absolute abundance of *G. pectinatus* within the water column than these environmental parameters as such. While temperature, salinity and associated environmental parameters will exert an influence upon the development of prey populations, thereby exerting an indirect influence upon the nature of the foods available, no direct influence of these parameters was discernible. Temperature associated interactions may influence food quality and availability (Anderson and Cummins, 1979). Salinity may influence the availability of zooplankton prey of *Neomysis mercedis* (Siegfried and Kopache, 1980). High salinity may have limited the population density of *T. chiltoni* during this study (Chapter 3). It is therefore interesting to note that adult *T. chiltoni* ingested a large quantity of food at Site 3 in February when the salinity reached 14.7‰, the highest recorded for this study. Unfortunately, when juvenile mysids were present at a site of low salinity, too few juvenile mysids were present at sites of high salinity to compare their diets; however, it was found that a limited number of post-larval mysids living at higher salinities ingested less food than mysids dwelling in less saline conditions in January. High salinity may therefore influence ingestion by juvenile mysids. A combination of bright sunlight and clear water, which would produce relatively high light intensities just above the substrate (where the mysid is found by day), did not appear to depress the feeding of *T. chiltoni*. The effect of night-time is unknown at present.

While the volume of food ingested was influenced by the concentration of the food resource, the turbidity of the water column was the only physical parameter shown to exert a strong influence on ingestion by *T. chiltoni* directly. The temperature and salinity of the water probably exerts indirect influences on the feeding of *T. chiltoni*, through effects on nutritional history and differences in growth (Raymont and Gross, 1942; Sutcliffe *et al.*, 1981), ingestion rates (e.g., Burns, 1969; Burns and Rigler, 1967; Gliwicz, 1977), incorporation rate (Bell and Ward, 1970), digestion rate (Molnar and Tolg, 1962) and the nutritional benefit to be derived from macrophyte detritus (Anderson and Sedell, 1979; Godshalk and Wetzel, 1978; Sutcliffe *et al.*, 1981).

Animals may switch between different habitats as a seasonal response to the availability of food in different environments (Horton, Rowan, Webster and Peters, 1979). The various populations of *T. chiltoni* sampled in Lake

Ellesmere showed considerable individual variation at times, especially in length, a parameter previously shown to influence ingestion. Dietary selection is not a constant in *Mysis relicta*, but is a variable parameter dependent on specific characteristics of the predator, prey and habitat (Rybock, 1978). Seasonal differences in selectivity based upon variations in the size structures of the mysid population have been implied previously (Edmondson and Murtaugh, 1980).

Not only does the habitat of an animal influence ingestion, but feeding methods may also vary. *Hemimysis lamornae* may filter-feed on smaller foods or grasp larger particles, and probably can filter-feed continuously (Cannon and Manton, 1927). A crustacean may vary its filtration rate as a response to food concentrations (e.g., Frost, 1972, 1975, 1977; McQueen, 1970; O'Connors, Briggs and Ninivaggi, 1980; Poulet, 1973). The ingestion by the individuals and populations observed may therefore be the result of interacting responses to a wide range of environmental parameters.

5.3.3 Food Consumption and Physical Diet Selection from the Food Resources

The purpose of the following discussion is not to describe the seasonal variations in the nature of the diet of *Tenagomysis chiltoni*, but to consider site-specific and time-dependent changes in the food resources which appear to be influencing ingestion by *T. chiltoni*. Specific items of the diet of *T. chiltoni* will have a specific probability of capture (Boyd, 1976), which is independent of the other food items present when elective, rather than selective, feeding is operative.

The ingestion of larger prey is sometimes favoured as they may provide larger rewards per unit search time (MacArthur and Pianka, 1966) but may not be taken due to the high probability of injury to a delicate consumer during encounters with active prey. In Lake Ellesmere the largest prey ingested by *T. chiltoni* are benthic. Within the mud there are many possible prey items, which are normally not available as it has been observed that *T. chiltoni* does not search the sediment for foods, as does *Hemimysis lamornae* (Cannon and Manton, 1927) and *Neomysis integer* (Parker and West, 1979). The benthic food resource is assessed from foods frequently ingested and occurring in the top 2 cm of the substrate, whereas *T. chiltoni* takes benthic food items only from the sediment-water interface. This limitation, necessitated by practical considerations, restricts the applicability of the results obtained to this study. However, if the availability of organisms

occurring at the interface is proportional to the availability of organisms known to occur in the substrate, then comparisons made between the diet of *T. chiltoni* and the benthic food resource are valid. In this study food abundances are presented as volumes, which may be less variable than numerical determinations (Strauss, 1979).

Mysis relicta and *Neomysis integer*, of similar adult length to *T. chiltoni* (Mauchline and Murano, 1977) ingest insect tissues (Mauchline, 1980), as does *Tenagomysis* sp. (Marples, 1962), and *M. relicta* can consume chironomid larvae (Lasenby and Langford, 1973). Only a limited number of mysid species are likely to encounter live chironomid larvae because most mysids and few chironomids live in saline environments. The presence of chironomid tail spines in the stomachs of *T. chiltoni* suggested that chironomid larvae were ingested more frequently than shown in Figures 16 to 19. The ingestion of *C. zealandicus* tissue was, however, sporadic and limited to mysids greater than 11 mm in length. *T. chiltoni* tended to consume only the smallest instars of *C. zealandicus*, which normally dwells within the substrate and is not available to *T. chiltoni*. The occasional lack of muscle tissue, or the distinctive digestive tract contents of *C. zealandicus*, in association with chironomid fragments, suggests that differential gut passage times may apply for different tissues of *C. zealandicus*, in addition to differences (shown to exist previously) between the gut passage rates of mandibles and labial plates. Differential gut passage and digestion rates are a common source of error in studies of diet (Berg, 1979; Hill, 1976; Nadin-Hurley and Duncan, 1976; Strauss, 1979). The possibility of such sources of errors in the evaluation of the contribution of *Chironomus* to the diet of *Tenagomysis chiltoni*, combined with the lack of agreement between the variations in density of *Chironomus* and its ingestion by *T. chiltoni*, recommended its exclusion from the calculations of the benthic food resource. An exception occurred at Site 1 in December 1979 when a large volume of chironomid tissue ingested was associated with the presence of large numbers of early instar *Chironomus* near a reed bed. The association with chironomid size and density at other times was moderate or weak.

Various factors may cause the discrepancy observed between the availability, in relative and absolute terms, and the ingestion of *Paracorophium lucasi*. The ingestion of the amphipod *P. lucasi* has been shown previously (Chapter 4) to depend on the size of the amphipod and of *T. chiltoni*. In a laboratory experiment, five adult mysids consumed only ten out of fifteen amphipods available within 24 hours, even though exposed

to these high prey densities without cover and showed no apparent visual response to the amphipods. The amphipods could collide with the region of the first and second endopods and still escape. It is therefore probable that the amphipod is not particularly susceptible to attacks from *T. chiltoni*. In addition, a portion of the population of *P. lucasi* may spend part of their time within the substrate. Thus only a small fraction of the amphipod tissue present may be available for ingestion by *T. chiltoni*. Benthic food resources may all have similar homogeneity of distribution (Downing, 1979), but also may exhibit differential clustering (Pyke *et al.*, 1977). The benthic sampling programme partially compensated for clustering by combining sub-samples.

The patterns of the ingestion of the harpacticoid copepods, *Braniola canterburyensis* and *Tachidius* sp., and the ostracod *Gomphocythere duffi* exhibit interesting differences when compared with their availability in the benthic food resource. The proportions of these species consumed by *T. chiltoni* show decreasing association with the availability of *B. canterburyensis*, *Tachidius* sp. and *G. duffi* (in that order); decreasing electivity is also apparent. While the larger harpacticoid, *Tachidius* sp., may be less easily captured by *T. chiltoni* than *B. canterburyensis*, which would affect their relative electivities (MacArthur and Pianka, 1966), the less mobile ostracod would be expected to fall prey to *T. chiltoni* more easily than *B. canterburyensis*. That it does not, and the lack of association between its abundance and consumption, suggests that *G. duffi* is for some other reason less available than either of the harpacticoid copepods. Low selection may be due to low encounter and consumption rates (Strauss, 1979). The most probable explanation of this phenomenon is that *G. duffi* is largely unavailable to *T. chiltoni* because it occurs relatively more frequently within the mud than at the sediment-water interface, compared with either harpacticoid. *Braniola canterburyensis* was more abundant than *Tachidius* sp. at most sites, and was consumed more frequently. *B. canterburyensis* has a higher and less variable electivity than *Tachidius* sp., suggesting that it may occur at the surface of the substrate with a higher frequency, and with greater consistency, than *Tachidius* sp., relative to its occurrence within the sediment. Abundance, capturability and microhabitat of the smaller benthic prey items may therefore interact with the feeding habits of *T. chiltoni* to influence the observed electivities of the prey species (as shown for other animals by Newsome and Gee, 1978; Nybakken and Eastman, 1977; Schnack, 1979).

The contribution of benthic animals to the diet of *T. chiltoni* was small considering their generally high abundances. This inconsistency was probably largely due to a combination of two factors: that the greater proportion of some animals occurred within the sediment (and were hence unavailable to *T. chiltoni*), and the low capturability of some prey items.

The water column food resource contained only a single species of animal eaten by *T. chiltoni*, the calanoid copepod *Gladioferens pectinatus*. Despite very low relative and absolute abundances, compared with other food sources, at most sites and sampling times during this study, *G. pectinatus* was frequently ingested in comparatively large proportions. In early 1980 the relative proportion of *G. pectinatus* in the diet of *T. chiltoni* increased noticeably, particularly at Sites 1 to 3 where greater absolute abundances of *G. pectinatus* were present within the water column. The fluctuations in the abundance of *G. pectinatus* are reflected as fluctuations in its consumption by *T. chiltoni*. The abundance of a food resource should determine its availability for ingestion, and therefore bear more resemblance to the amount of ingestion of that food by an animal than its relative abundance (Holling, 1965; Houston, 1973; Pulliam, 1974). As the absolute abundance of many benthic foods is much greater than the abundance of *G. pectinatus*, it would be expected that these benthic animal foods would be consumed with greater relative frequency than was observed. However, the higher costs of searching a given volume of mud for food, compared with a volume of water, may make the former an unprofitable strategy (Pyke *et al.*, 1977), even if it is within the capacities of the organism, as Cannon and Manton's (1927) work on *Hemimysis lamornae* suggests.

When site specificity in the consumption of *G. pectinatus* was examined it was found that the consumption of this species by *T. chiltoni* was generally greatest at the more saline sites, and that consumption was related to the absolute abundance at all sites. A marked fluctuation in the absolute abundance of *G. pectinatus* within the water column resource often caused variation in the ingestion of *G. pectinatus*, apparently due to a random component, such as unmeasured aggregations of *G. pectinatus*. Patchiness in the distribution of *G. pectinatus* raises its abundance locally relative to its abundance in the ecosystem, and can lead to increased ingestion (MacArthur and Pianka, 1966). A positive correlation between mysid ingestion and copepod abundance was found over a wide range in prey density (Lasenby, 1979; Rybock, 1978). Fourteen out of the 25 species of mysids considered by Mauchline (1980) consumed Copepoda (Table 11, Chapter 7).

All other frequently occurring components of the diet of *Tenagomysis chiltoni* are common to both the benthic and water column food resources. It appears that *T. chiltoni* is feeding principally from the water column, but possibly also from a very thin layer near the surface of the sediment. The best established relationship between supply and utilisation of a food resource is for the only animal species in the water column, and that the only established relationships of this type within the benthic food resource are for species probably occurring close to the sediment water interface. This conclusion is supported by aquaria observations, by the relationship between the quantity of food in the water column and the volume present in a stomach and by suggestions on the relative costs of searching for food in sediment and in water.

Many diatoms present, including the principal members of three of the four diatom groups most important in the diet of *T. chiltoni*, grow as single epiphytes or chains, upon or within filamentous algae, macrophyte detritus or sedimentary particles. These three groups account for 83% of the diatoms ingested by *T. chiltoni*. The ingestion of diatoms by *T. chiltoni* will therefore depend, in part, upon seasonal variations in the growth or suitability of appropriate substrates. When the substrate is also ingested (e.g., macrophyte detritus or filamentous algae) a correlation would be expected between the volumes of substrate and of epiphytes ingested. Such correlations seem to occur quite frequently throughout much of the study period, particularly between the ingestion of diatoms and filamentous algae. A single species of diatom of group J (probably *Hyalodiscus* sp.), contributed 77% of the volume of diatom tissues ingested by *T. chiltoni*, and would be expected to show seasonal variations in abundance. This species is epiphytic on sand grains, macrophyte detritus, filamentous algae and gastropod shells. Seasonal variations in the supply of these different substrates, and probable differences in the growth rates of filamentous algae and diatoms, may account for the weaker associations observed at times between the ingestion of diatoms and macrophyte detritus or filamentous algae. *T. chiltoni* may also be capable of rejecting the less desirable substrate and retaining the diatoms (*Praunus* sp., Tattersall and Tattersall, 1951). The sites at which least relationship exists between the ingestion of filamentous algae and diatoms between November and January are, interestingly, those sites at which the mysid population was dominated by post-larval and juvenile mysids of length classes which ingested noticeably smaller volumes of diatoms (Sites M, 1 and 2). At this time of

the year the weakness of the association may result from an interaction between the mysid population and the relative availability of diatoms and filamentous algae.

Tenagomysis chiltoni appeared to ingest the larger diatoms present, or those associated with other particles which increased their effective size. *Mysis relicta* only ingested the largest size classes of diatoms present (Bowers and Grossnickle, 1978), and size selectivity is also apparent in the ingestion of diatoms by *Neomysis mercedis* (Siegfried and Kopache, 1980). The diatom food resources sampled contained numerous small diatoms not normally ingested by *T. chiltoni*. This observation, and the unpredictably variable response of a mysid to diatom concentration (Lucas, 1936), in conjunction with factors previously discussed, explains the low degree of relationship between the diatoms present in the water column and benthic food resources, and their consumption by *T. chiltoni*. As post-larval mysids consumed greater proportions of the intermediate-sized diatoms than adult mysids, it was not possible to define the food resource in terms of effective accessibility (Berg, 1979) for mysids of all lengths.

In other studies of the feeding of the Mysidacea (e.g., Mauchline, 1980; Kost and Knight, 1975), "detritus" may be defined as unidentifiable amorphous materials which may be derived from fragmented algae or crustacean body fluids (Siegfried and Kopache, 1980). Foods ranked above macrophyte detritus contributed only 27% of the total volume ingested by *T. chiltoni* during this study, however, the nutritional value of these foods to the mysid is probably greater than this figure would suggest due to their greater calorific and nutrient contents.

The consumption of macrophyte detritus by *T. chiltoni* was related to the supply of macrophyte detritus in the water column, and normally only showed moderate changes in the proportions consumed when an opposite change in the consumption of other foods occurred; this is possibly due to variations in the feeding response of a mysid in response to changing availability of food (Edmondson and Murtaugh, 1980). Feeding rate is normally proportional to food concentration up to the limitations imposed by an organism's capacity to ingest (Frost, 1972; Rigler, 1961; Small, 1969); in Crustacea using alternative feeding mechanisms the question of which, if any, of the alternative feeding mechanisms will show reduced filtration rate first when the animal is close to satiation, is of relevance to, but unanswered by, such observations, as it is not known which method *T. chiltoni* employs to capture detritus. The answer to this

question may contradict observations on Copepoda that electivity is independent of particle concentrations (*Calanus helgolandicus*, Schnack, 1979) as it is a probability function (Boyd, 1976). *T. chiltoni* can, however, probably be included in the statement that mysids take all foods which are more or less immediately available (Raymont *et al.*, cited in Kost and Knight, 1975), and the statement that availability will consequently govern resource utilisation by a mysid (Kost and Knight, 1975).

Macrophyte detritus was a large or dominant component in the diet of *T. chiltoni* at most sites, but the quantity and proportion consumed was dependent upon local conditions. Detrital quality is influenced by the effects of allochthonous and *in situ* decomposition (Teal, 1962), acting differently upon detritus of different origins (Gasith and Lawacz, 1976), according to the conditions in the environments encountered prior to ingestion (Anderson and Sedell, 1979; Levinton, 1972; Sutcliffe *et al.*, 1981). Detritus is not a single food source, but a collection of particles having a variety of origins and histories, a heterogenous assortment of plant fragments of varying nutritional value. The mysid may therefore be selecting within this resource as well as between detritus and other resources. Seasonal variations in the concentration of refractory materials within the detrital food resources (Olah, 1972) suggested that the mysids' selection for this food resource may have varied during the annual cycle. *T. chiltoni* ingested the greatest proportion of macrophyte detritus during the winter when the detritus was least nutritious (Olah, 1972). Detritus may therefore have been consumed in larger proportions because of its abundance or the scarcity of other foods. The increased relative and absolute abundance of macrophyte detritus in both water column and benthic food resources at all sites over the winter months, will tend to offset the effects of any decline in the quality of the detrital food resources on *T. chiltoni* over the winter period. There are, however, many sources of variability within the detrital food resource which may affect an organism's selection of it. There are also changes in the digestive processes of fish which can alter the utilisation efficiency of the detrital food resource relative to other food resources (Kawai and Ikeda, 1972). In view of these factors, and the interaction of moderate sample sizes (30 specimens) with the marked individual variation observed in ingestion rates in this study, and others (Lasker, 1966; Kato *et al.*, 1979), a good relationship exists between the proportion of macrophyte detritus consumed by *T. chiltoni* and its absolute and, to a lesser degree, relative abundance in the water column. The weaker relationship between consumption and the abundance of detritus within the benthic food resource is further evidence of the lesser

availability. Macrophyte detritus is an important component of the diet of *T. chiltoni*, which may be efficiently utilised (*Mysis stenolepis*, Foulds and Mann, 1978), and make a major contribution to the organism's nutritional needs without adversely influencing growth (Kajak *et al.*, 1977). The contribution of macrophyte detritus to the diet of *T. chiltoni* is more stable between different sites and sampling periods than any other food. The consumption of more highly ranked foods by *T. chiltoni* is dependent on food concentration (this study), and the associated influences of prey reduction upon ingestion (Charnov *et al.*, 1976). In view of the limited predatory ability of mysids (Siegfried and Kopache, 1980) upon organisms which formed a large proportion of the available foods of higher rank than macrophyte detritus, macrophyte detritus may play an important role as a staple diet of *T. chiltoni* due to its abundance and the consistency of its supply in the lake. Nine of the 25 mysid species reviewed by Mauchline (1980) consumed "terrigenous material".

At most times the ingestion of filamentous algae was proportional to its abundance within the water column food resource, although the quantity ingested was partially dependent on interaction between the abundance of filamentous algae within the water column food resource at any time and the population present. When young mysids were present, an increase in the proportion of filamentous algae ingested was observed; this was due, in part, to the contracted range of food types they were capable of ingesting. While in aquaria, adult *T. chiltoni* did feed upon filamentous algal mat when first introduced to the food, the mysid later ignored the filamentous algae even when unfed for several days. This suggests that the mysid may have been utilising fragments of algal clusters and smaller broken strands. As these are more likely to be suspended in the water column and would be easily captured by *T. chiltoni* in the lake, and young mysids may occur higher up in the water column than adults (Mauchline, 1980), this may offer a partial explanation of the higher ingestion of filamentous algae by juvenile mysids compared with adults.

5.3.4 Some General Considerations on the Diet

Ingestion by non-selective benthic carnivores may not be related to their prey density in the benthos (Fahy, 1972), or other food resources, as the response of each individual may differ markedly, and even the response of the same individual in successive time periods (Kato *et al.*, 1979), as a result of individual experience of a heterogenously distributed resource. Sampling error is proportional to the volumes and numbers of substrate samples examined for potential prey species (Downing, 1979). Each mysid will only

search small volumes of substrate to assess prey density (due to energetic constraints, Holling, 1965) and may search a limited number of sites, so that there will be variability in the predator's rate of encounter with a prey species and hence its rate of reward. The small sample number taken at each site will thus result in some random error in the determination of the diet of the whole population at that site. Errors in the estimation of resource densities and availability may also produce errors in the assessment of the relation of the observed ingestion to the resource. However, if similar levels of aggregation occur in most species of animal (Downing, 1979), the interspecific variability in the electivities of *T. chiltoni* responding to any species of animal prey would be similar. This was not the case in the present study. The best explanation of this finding is that the resource was not defined by the experimenter as the mysid defined it. During the day, *T. chiltoni* appears to search the sediment-water interface for food, not the sediment itself as does *Hemimysis lamornae* (Cannon and Manton, 1927). In aquaria the mysid does not search the sediment for food, or show an ability to move quantities of sediment, as do *Gastrosaccus* spp. (Mauchline, 1980) and *Neomysis integer* (Parker and West, 1979). The ingestion of benthic organisms by *T. chiltoni* therefore appears to occur on the sediment surface, where those organisms ingested may have different densities and distributions compared with their occurrence in the top 2 cm of substrate. Where it was known that an animal occurred within the water column in the region occupied by *T. chiltoni*, a highly selective relationship was found between the absolute abundance of that organism, *Gladioferens pectinatus*, and its consumption by *T. chiltoni*. In several other mysids consumption of Copepoda is proportional to the copepods' abundance (Lasenby, 1979; Rybock, 1978; Siegfried and Kopache, 1980), but the relationship between the proportion consumed and the proportion available depends on the prey species taken (Threlkeld *et al.*, 1980). The volume of copepod ingested will also depend on the size of the mysid, as the volume of water swept clear of food shows a close relationship to the consumer's body length (Downing and Peters, 1980), and the relative abundance of alternative prey (Newsome and Gee, 1978). The above factors, in conjunction with mysid population densities, will determine the environmental impact of the mysid upon the prey populations present; the impact of *T. chiltoni* on environments in Lake Ellesmere cannot be assessed until information on the gut passage rates of food within the digestive tract is available for different water temperatures as has been determined for other species (Elliott, 1979; Molnar and Tolg, 1962; Vahl, 1979).

Electivity of a predator-prey association has been defined by a number of authors for use as an index of affinity of a predator and prey (e.g., Chesson, 1978; Ivlev, 1961; Paloheimo, 1979; Rapport and Turner, 1970; Strauss, 1979). To compare the electivities of a predator preying on different species, errors in the assessment of the food resource must be independent of sampler selectivity and net avoidance (O'Brien and Vinyard, 1974); these errors are rarely negligible. The functional response of a predator to prey density is crucial to an understanding of predator-prey relationships (Holling, 1965); this response is not normally linear, but a complex interaction of prey density and accessibility (Rapport and Turner, 1970; Strauss, 1979), and a predator's feeding abilities (Paloheimo, 1979; Pyke *et al.*, 1977) and the abundances of alternative prey types at any given time (Berg, 1979; Carefoot, 1973). The interaction between any two of these variables is unlikely to be linear, and the relationship of the quantity ingested and the quantity available is frequently markedly non-linear (Emlen, 1966; Fahy, 1972; Holling, 1965; Mullin and Stewart, 1975). As a complex interaction of non-linear responses cannot be described by a simplistic linear ratio, no attempt was made in this study to enumerate the relationship between the mysid and the density of *G. pectinatus* present. This relationship was, however, highly elective.

It is interesting to note the exceptionally low ingestion of juvenile *G. pectinatus* which were, at times, dominant. The two feeding mechanisms of mysids demonstrated by Cannon and Manton (1927) and others will probably have different clearance rates. Changes in the food concentrations present may cause changes in the feeding methods used, resulting in changes in electivities (Edmondson and Murtaugh, 1980). The observed changes in electivities between different food types may well in part be due to these electivity differences. However, the low degree of predation on early stages of *G. pectinatus* is unlikely to be a result of changes in feeding behaviour, as a result of food concentration, as copepodites were not ingested frequently even when abundant. It is more likely to be due to size selectivity. Siegfried and Kopache (1980) observed no ingestion of copepodites by *Neomysis mercedis*.

The selection of foods from a given resource by crustacean filter-feeders depends more upon a probability function (Boyd, 1976), dependent on the intersetular spacing on the feeding appendages (Nival and Nival, 1976), than a decision to attempt to capture a food particle. However, *Hemimysis lamornae* may regulate the size of the suspended food particles filtered by altering the height at which it swims above the substrate (Cannon and

Manton, 1927) and thus may exhibit behavioural selectivity. *Tenagomysis chiltoni* ingested greater proportions of small more friable diatoms in post-larval stages, but principally larger diatoms in later stages, as did *Mysis relicta* (Bowers and Grossnickle, 1978). These larger diatoms were frequently colonial or attached, increasing their effective particle size (Bevan *et al.*, 1978), which may have been fragmented by the feeding of the mysid, increasing the food available to copepods (Bowers and Grossnickle, 1978) and other small particle feeders. Parsons *et al.*, (1967) recorded the ingestion of different size ranges of diatoms by furcilial and adult *Euphausia pacifica*.

No precise relationship existed between the density of diatoms in the water column and the consumption of diatoms by *T. chiltoni*. Such a relationship has been found on other crustaceans (e.g., Cushing, 1959; Frost, 1977; Rigler, 1961), and was partially dependent on the morphology and concentration of the filtered particles (McQueen, 1970). This may have been due partly to variation in the degree of association of the food particle with a substrate (Gray and Ward, 1978), food resource sampling errors (O'Brien and Vinyard, 1974), and the absence of any allowance for the differential size selectivity of mysids grazing diatoms in calculating the available food resources.

The consumption of filamentous algae by *T. chiltoni* showed a resemblance to the abundance of these algae within the food resource, after allowance was made for ontogenetic changes in the diet and selective effects on ingestion. It is possible that not all the filamentous algae present were obtainable, and that younger smaller growths of algae were preferred (as in insect larvae studied by Gray and Ward, 1978), by the mysid. The ingestion of filamentous algae is moderate compared with their availability within the water column. As filamentous algae are easily collected by *T. chiltoni*, this may be partially due to an inhibitory effect upon ingestion (Gliwicz, 1977). The high consumption of filamentous algae may be a result of their abundance in an environment in which animal prey are rarely successfully encountered and in which the large resource of diatoms is only partly utilised (*Mysis relicta*, Bowers and Grossnickle, 1978).

The proposal that macrophyte detritus is a food of *T. chiltoni* (Chapman and Lewis, 1976) has been verified. While macrophyte detritus has been recorded as a component of the diets of several mysids (Mauchline, 1980), its importance in mysids' diets has only been accurately assessed for *Taphromysis bowmani* and *Mysidopsis almyra*, in which plant detritus comprised 26% and 31% respectively of the volume of foods ingested (Odum and Heald,

1972), a noticeably lower proportion than was consumed by *Tenagomysis chiltoni*. This variation between species may be a result of interspecific variations in ingestion and behaviour, as *Taphromysis bowmani* and *M. almyra* occur within similar environments, or a product of variations in the food resources available to each mysid (Edmondson and Murtaugh, 1980; Kost and Knight, 1975; Rybock, 1978; Siegfried and Kopache, 1980; Threlkeld *et al.*, 1980), as was found for different populations in this study. As Lake Ellesmere may trap detritus from inflowing rivers, the large volumes consumed by the dense population of *Tenagomysis chiltoni* present are of interest to the ecology of the lake as some organisms may mechanically (Mare, 1943) and biochemically (Foulds and Mann, 1978) aid detritus oxidation. Bacteria may process detritus to a usable form and are themselves food (e.g., Anderson and Sedell, 1979; Fenchel, 1972; Hargrave, 1970, 1972; MacGinitie, 1932, 1935; Sutcliffe *et al.*, 1981). In Lake Ellesmere, as elsewhere (De Sylva, Kalber and Shuster, 1962), plant detritus may become so abundant that it forms a mat above the sediment. At most sampling periods macrophyte detritus was an important constituent of the food resource and diet of *T. chiltoni*. The potential importance of mysids as converters of detritus to animal tissue can hardly be exaggerated in estuaries (Percival, 1929), and *T. chiltoni* may well play a similar role in Lake Ellesmere, reworking and suspending the organic matter sink (Levinton, 1972) above the sediment.

Tenagomysis chiltoni did not ingest appreciable volumes of sediment, as do several other mysids (Mauchline, 1969, 1970a, 1970b, 1971b, 1971c; Odum and Heald, 1972), possibly because it is not searching the sediment for food particles, as was for example *Hemimysis lamornae* (Cannon and Manton, 1927). This observation may therefore further substantiate the conclusion that *T. chiltoni* is not feeding upon organisms within the substrate.

Having analysed the reaction of *T. chiltoni* to the different foods available, it can be seen that *T. chiltoni* feeds on foods which are grasped individually for example Copepoda (Siegfried and Kopache, 1980) and probably Amphipoda and Ostracoda, and foods which are filtered, for example, diatoms (Lucas, 1936). Macrophyte detritus and algal filaments may be trapped by either method according to the dimensions of both the food particle and the predator, but are probably normally captured on the filter-feeding apparatus, as the mysid ignored larger fragments of grass and filamentous algae in aquaria but still fed actively. *Tenagomysis* spp., however, have mouthparts capable of masticating macrophyte detritus (Chapman

and Lewis, 1976). It is apparent from the large ingestion of planktonic copepods, diatoms and other foods that both the filtratory and raptatory feeding mechanisms can be used very effectively at times. Whether the mysid may vary the functional response curves to different food concentrations of each feeding mechanism, independently of each other, is an important question, as this will influence the quantity of food collected by each mechanism, and may also influence the quality of their diet. Edmondson and Murtaugh (1980) suggest that "mysids may alter their [raptatory] feeding behaviour in response to changing availability of prey", while Cannon and Manton (1927) stated that *Hemimysis lamornae* filter fed continuously, but did not specify whether it filtered foods with a constant clearance rate. Subsequent work shows that less elaborate feeders, including many Crustacea (e.g., Nival and Nival, 1979; Porter, 1977; Randløv and Riisgård, 1979), vary their clearance rate in response to variation in food particle shape and size, and many other factors (McMahon, 1965). The more closely related euphausiid shrimps (Schram, 1981), also vary their clearance rate as a response to the external environment (Kato *et al.*, 1979; Lasker, 1966; Pavlov, 1971). As the ingestion of *G. pectinatus* and diatoms, captured by the two different mechanisms, bore little resemblance to each other in similar relative abundances, the two mechanisms appear to be independent of each other.

Food particle rejection has been observed within the Order Mysidacea (Cannon and Manton, 1927; Tattersall and Tattersall, 1951). However, as both particle types were palatable to the mysids present, there is no reason why rejection should have occurred. Laboratory experimentation designed to resolve this question is needed; it seems, at present, that the mysid may vary its feeding response as an adaptation to its environment.

The degree of electivity observed for a food particle is not a constant in mysids generally (Rybock, 1978), or in *T. chiltoni*. It is an interaction of developmental and physiological characteristics of each individual constituting the mysid population with the accessibility, capturability, and ingestibility of a food, and possibly coexisting foods. In the case of *T. chiltoni*, considerable site to site and month to month variation was observed in the selected diet. Considerable local variations were observed in the absolute and relative availability of foods in Lake Ellesmere, as in other environments (e.g., Gray and Ward, 1978; Siegfried and Kopache, 1980), these caused associated changes in the diet of *T. chiltoni* where the foods present were available and desirable. Numerous authors have noted the influence of food availability upon ingestion (e.g., Cushing, 1959, 1962; Kost and Knight, 1975; Moore, 1977)

and that this may influence the growth of animals (Ross, 1981), including mysids (Morgan, 1980; Olsen, 1980). The observed ingestion is therefore the result of the multiple interactions of different factors which support and expand upon the basic generalisation of Muttkowski and Smith (1929) that local conditions beget local results. The behaviour and feeding mechanisms of *Tenagomysis chiltoni* probably partially restrict it to a relatively poor diet in the presence of abundant supplies of foods which are probably more nutritious than those consumed. Diet is the observable product of evolution acting on blends of suitability determined by several factors (Carefoot, 1973), and is limited by the heterogeneity of the environment (Emlen, 1968).

CHAPTER 6

SEASONAL VARIATION AND SITE SPECIFICITY OF THE DIET

6.1 INTRODUCTION

In the preceding chapters the influence of various intrinsic and extrinsic factors on the diet of *Tenagomysis chiltoni* were discussed with reference to the Lake Ellesmere system. This chapter considers general seasonal variation and site specificity of the diet of *T. chiltoni* in Lake Ellesmere by combining the results from all sites in each month, and all the results from each site.

6.2 RESULTS

When the stomach contents of mysids from all four sites are combined for each sampling period a much clearer picture of the seasonal changes in feeding emerges. Apparent and real variations in diet caused by site specific differences due to both experimental errors and differences in ingestion brought about by variations in the nature of the food resources available are reduced. Unfortunately it is not possible to present percentages for combined water column and benthic food resource data to complement the diet results (Table 9, Fig. 20), as variations in the total quantity of food present at individual sites tended to weight the food resource proportions unduly towards the results from a single site or sites.

The proportion of diatoms ingested at any sampling period was remarkably constant, especially as a single diatom group, Group J, contributed 78% of the total volume ingested. This group was probably composed of a single species of the genus *Hyalodiscus* and would have been expected to show more seasonal variation in its abundance than was observed, probably with consequent changes in the proportion ingested. The four diatom groups which constituted by far the greater proportion of the diatom fraction in the diet are all either unusually large diatoms (*ca.* 100 µm diameter) and solitary, or colonial or epiphytic and therefore with a larger effective particle size, increasing the probability of their capture by the maxilla (Nival and Nival, 1976). No other diatoms of these sizes or habits were found in Lake Ellesmere during this study. All other diatom groups ingested were eaten in small proportions, and were found in some stomach

Table 9. Seasonal variation in the percentages and volume of foods ingested.

Food Type (%)	1979 SEP.	NOV.	DEC.	JAN.	FEB.	MAR.	1980 MAY	JUNE	JULY	AUG.	OCT.
Diatoms	17	18	9	15	12	11	18	15	8	16	7
Filamentous algae	6	45	39	31	16	2	20	12	11	14	14
Macrophyte detritus	33	32	51	49	49	16	49	63	69	57	63
G. pectinatus	2	5	1	4	21	7	9	8	6	9	2
Harpacticoid copepods and ostracoda	2	0	0	0	1	2	1	1	3	3	8
P. lucasi	1	0	0	1	1	1	3	1	3	1	4
C. zealandicus	39	0	0	0	0	61	0	0	0	0	2
Individual change in volume ingested since previous sample	-	0.6	6.3	0.6	0.9	1.6	0.8	0.7	1.0	0.9	0.6
Size range of mysids (mm)	8-17	2-15	2-16	2-12	2-14	2-14	4-15	5-16	5-17	5-17	8-17
Population change in volume ingested since previous sample	-	0.7	16.2	0.8	0.5	0.5	0.3	1.0	0.6	0.4	0.4

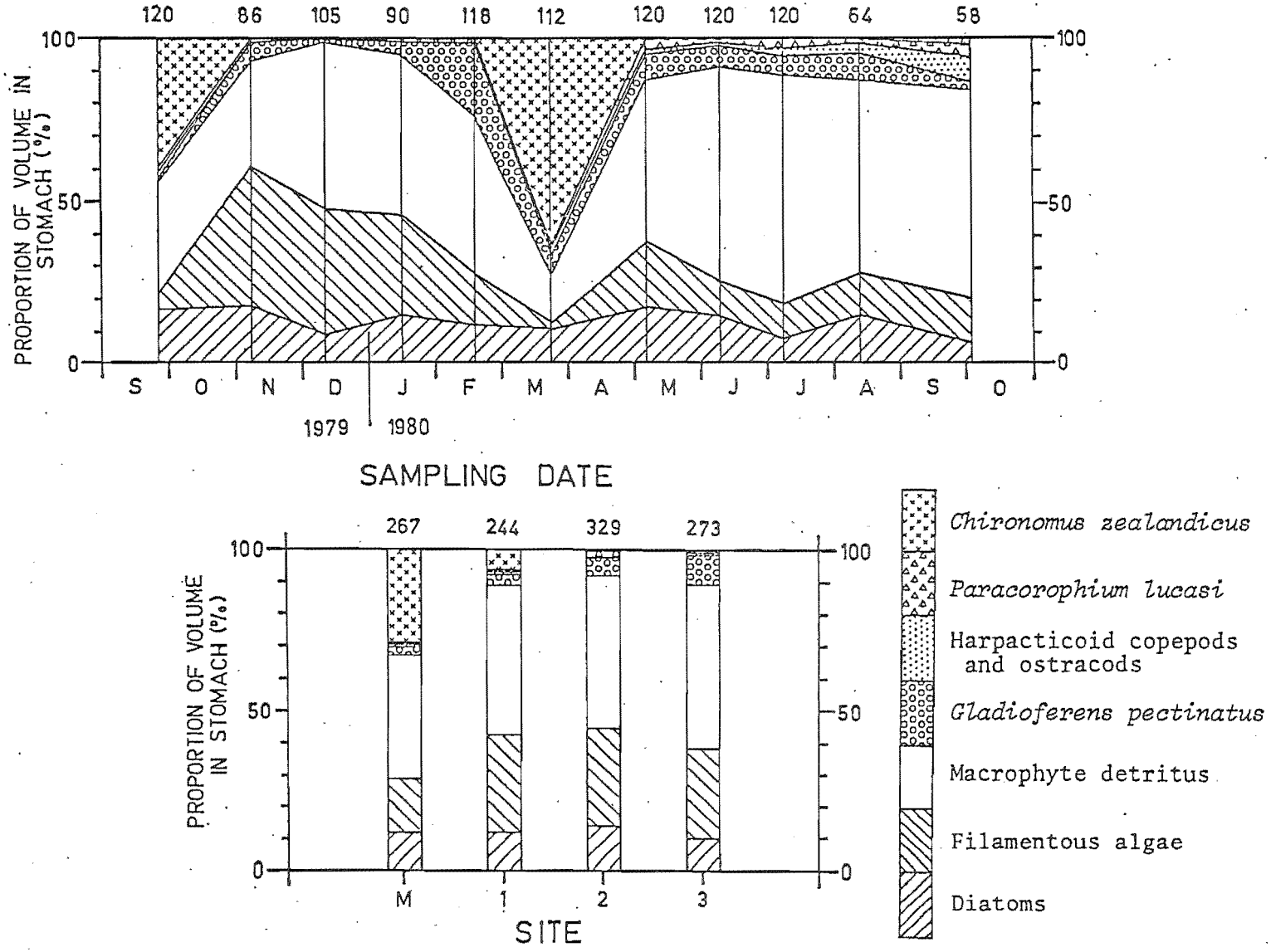

Fig. 20 Seasonal and site-specific variations in the diet of *Tenagomysis chiltoni*.

samples as epiphytes of macrophyte detritus, so were probably captured and ingested attached to a larger detrital particle. Solitary diatoms of Groups A, B and K were rod-shaped and although relatively large (50-200 µm) when measured along their long axis, were narrow measured on their shorter axis. These diatoms were rarely ingested in quantity, despite moderate abundances within the food resource. Their capture on the endite of the maxilla may depend on their orientation in the passage of water passing through the filtering setae. The smaller juvenile mysids ingested slightly higher proportions of these diatom groups; this may reflect seasonal changes in the abundance of these diatom groups, a stronger tendency for juveniles to filter-feed, or differences in the size spectra of the intersetular distances between juveniles and adults. However, only the larger diatoms present, and those attached to or forming larger particles, are ingested in large quantities.

Filamentous algae showed marked seasonality of abundance in the water column food resource samples. This seasonality was reflected in the proportions of filamentous algae ingested (Fig. 20). The maximum contribution of this food resource to the diet of *T. chiltoni* was 45% and occurred during November (Table 9). Much higher proportions of algae were ingested at some sites (e.g., Sites M and 1) at this time. The high proportion of filamentous algae eaten at this time is due in part to their increased availability, and partly to the more intensive utilisation of this resource by post-larval and juvenile mysids. As a mysid grew it extended the range of foods ingested and the proportion of filamentous algae eaten declined. At the same time, however, the abundance of filamentous algae within the food resource also declined and it is not therefore possible to attribute a degree of influence to either factor. In mysids present in the March samples, filamentous algae formed only 2% of the total volume of food eaten, the smallest proportion recorded during this study. This minimum would still apply even if *Chironomus zealandicus* was excluded from the calculation, on the grounds that the volume of chironomid tissue present was overestimated in March. Over the winter months filamentous algae contributed a moderate volume of tissue to the diet of *T. chiltoni*. Over the whole study period filamentous algae formed 27% of the volume of food present in the stomachs of the mysids in the population sampled. The feeding technique used by *T. chiltoni* to capture strands of filamentous algae is not known. While mysids in aquaria grasp clumps of filamentous algae and feed on the filamentous cluster, the clusters were subsequently ignored over a period of several days, during which no food was added.

T. chiltoni may, therefore, feed on the smaller strands and clusters of filamentous algae within the water column, possibly using a combination of raptatory and filtratory mechanisms. The resource was composed of several species of algae probably from among those listed in Hughes *et al.* (1974).

Macrophyte detritus was the single most important food of *T. chiltoni* during this study, contributing over 46% of the volume of food to the mysids' diet. The abundance of this resource was extremely variable within both the water column and the substrate. It was observed to form rafts of detritus on top of the substrate during calm weather and occasionally formed piles over 25 cm thick on lee shores. This detritus was heterogenous in origin but composed principally of grass fragments, many of which may have been washed from flooded pastures. When differentiation between monocotyledon and dicotyledon leaf fragments was possible, the ingested plant detritus particles were normally identified as monocotyledon leaf fragments. Generally, macrophyte detritus formed an increasing proportion of the volume of food ingested throughout the study, rising from 33% of the total volume ingested in September to about 60% of the diet over the last four months. Macrophyte detritus appeared to contribute similar proportions of tissue to the diet of *T. chiltoni* in September and November, between December and May, and between June and October (if chironomid tissue is excluded from the calculated diet for March, as the estimate of chironomid tissue ingested was probably excessive). There was no apparent correlation between changes in the proportion of macrophyte detritus ingested and preceding weather conditions, lake level, or seasonal environmental changes. Variation in the terrestrial supplies and transport of plant detritus does not therefore seem responsible, but the proportion ingested is proportional to the macrophyte detritus resource within the lake.

Gladioferens pectinatus contributed a small and variable portion to the mysids' diet until February and March when it contributed 21% and 18% respectively of non-chironomid foods ingested. The high proportion ingested in these months was related to the high proportions of *G. pectinatus* in the water column food resource at Sites 2 and 3. As noted earlier, these higher proportions may have been associated with the moderate to high salinities occurring within the lake at this time. The capture of *G. pectinatus* was probably effected by a raptatory feeding mechanism (as in *Neomysis mercedis*, Siegfried and Kopache, 1980). *G. pectinatus* contributed 6% of the total volume ingested by *T. chiltoni* during this study.

The total contribution of all harpacticoid copepods and ostracods to the diet of *T. chiltoni* was only 0.5%; *Braniola canterburyensis* contributed 0.3%, *Tachidius* sp. 0.1% and the ostracod *Gomphocythere duffi* 0.1% of the observed diet. The proportion of these groups ingested by *T. chiltoni* was small at most times of the year, but increased through the winter of 1980 to 8% of the diet in October.

The amphipod *P. lucasi* contributed less than 1% of the total volume ingested during this study. The proportion of *P. lucasi* tissue ingested increased in the second half of the study, but only comprised at most 4% of the diet of *T. chiltoni*. An association was found between mysid and amphipod lengths (Chapter 4), suggesting that the prey was taken live and was capable of escape. The low proportion of *P. lucasi* ingested, in relation to the large numbers present, suggests that either *T. chiltoni* was not attacking *P. lucasi* very frequently, or that most encounters with *P. lucasi* were unsuccessful, as suggested by observations in aquaria.

Chironomus zealandicus, according to calculations, formed 6% of the diet of *T. chiltoni* and contributed to the diet only during three months. In September 1979 at Site 1 and October 1980 at Site 2 abundant unidentifiable muscle tissue was associated with chironomid gut contents in the stomachs of some mysids. The calculated ingested volumes of chironomid tissue at these times probably approximately represents the ingestion by the mysid populations present. The ingestion of chironomid tissue in March at Site 3 was, however, calculated from a few mysid specimens in which *C. zealandicus* mandibles were present. In view of the absence of large volumes of chironomid muscle tissue, or sediment from the digestive tract of *C. zealandicus*, within the stomachs of these mysids the calculated volume of *C. zealandicus* tissue present is probably vastly overestimated. This belief is substantiated by the very large effect made on the estimate of the diet of March mysids (present at all sites) by a minority of mysids present at a single site, if these *C. zealandicus* are included; this comment applies to a lesser extent to the September sample, when some ingestion of *C. zealandicus* did occur.

It is interesting that in November and December when small juvenile mysids constituted most of the population of *T. chiltoni*, no benthic animal forms a noticeable component of the diet of *T. chiltoni* despite the presence of an increased abundance of benthic components of the diet at most sites and of some overwintered adult individuals capable of ingesting these animals. This phenomenon appeared to be associated with the observed change in the structure of the population but its persistence in January and February

suggests that it may also be associated with the increased availability of food within the water column at most sites over this period. After 1 March, increased proportions of benthic animals were ingested by mysids of a similar length range to those present in the preceding two months. As the suspended food resource became more depleted subsequent to the February sampling period, the phenomenon may well be associated with food availability.

There was little difference in the composition of the diet between different sites when all mysids sampled at that site were analysed as a group (Table 10, Fig. 20). The proportion of diatoms ingested by mysids at Site M is slightly higher than at other sites when *C. zealandicus* is excluded from the calculations. The proportions of filamentous algae, macrophyte detritus and harpacticoid copepods and ostracods ingested by *T. chiltoni* were similar at all sites, except at Site M where smaller proportions of filamentous algae were present. The fraction of the diet composed of *G. pectinatus* tissue increased towards the more saline regions of the lake. The numbers of *G. pectinatus* at sites of different salinity within the lake may be affected in two ways, in the long term by the salinity influencing suitability of the water column as a habitat, and in the short term by dilution of the resource already present by the influx of quantities of fresh water. The ingested quantities of *Chironomus zealandicus*, as calculated, decrease with distance from the less saline marsh site, Site M; but the calculated results may not represent the real situation.

Table 10. Site specific variation in the percentages and volume of foods ingested.

Food Type (%)	Site M	Site 1	Site 2	Site 3
Diatoms	12	12	14	9
Filamentous algae	18	31	30	29
Macrophyte detritus	40	46	48	51
G. pectinatus	3	4	6	10
Harpacticoid copepoda and ostracods	1	1	0	0
P. lucasi	0	1	2	1
C. zealandicus	26	5	0	0
Total volume of food present in all specimens (mm^3)	12.9	16.7	21.4	21.8

The volume of food ingested decreases markedly between Sites 3 and M and shows progressive reduction in the volume ingested at both intermediate

sites. These differences show a relationship to the salinity differences found between the different sites and may be a direct or indirect consequence of variations in the salinities experienced by *Tenagomysis chiltoni* and its foods within Lake Ellesmere.

6.3 DISCUSSION

It has been shown previously that ingestion by *T. chiltoni* is partly dependent on the length of a mysid, presumably because the potential of the mysid to masticate stronger structures and subdue more active prey increases with length (Chapter 4). Similar changes have been demonstrated in the diet of *Neomysis mercedis* (Edmondson and Murtaugh, 1980; Kost and Knight, 1975; Siegfried and Kopache, 1980). While developmental changes in the feeding of *Neomysis mercedis* have been suggested as factors influencing the diet of populations of mysids showing marked seasonal population cyclicity (Edmondson and Murtaugh, 1980), this study is the first demonstration of this effect within a single natural population of mysids in the field. While the size of individual mysids comprising a single population influences the ingestion by a population, size-specific differences in the diets of *T. chiltoni* in natural populations within Lake Ellesmere were not normally sufficiently marked to produce large variations in the ingestion of foods from the food resource available at a site as a consequence of changes in the population structure.

T. chiltoni ingested only the largest size range of diatoms and smaller diatoms when attached to larger structures. Bowers and Grossnickle (1978) recorded that *Mysis relicta* also ingested only the largest size range of diatoms present. This size selectivity is probably dependent on the structure of the maxilla (*Hemimysis lamornae*, Cannon and Manton, 1927; *Acartia clausi*, Nival and Nival, 1976). Diatoms ingested while attached to macrophyte detritus formed an insignificant fraction of the diet of *T. chiltoni*, and are not therefore an important source of epiphytic food of the mysid, as bacteria may be (Fenchel, 1970, 1972); the role of bacteria as a food component was not investigated in the present study.

The minimum particle size captured by *T. chiltoni* was greater than 45 µm (personal observation). Due to this large minimum size of particle retained by the maxillary filter the only bacteria which the mysid could have ingested would have been those growing on another particle, such as macrophyte detritus.

The utilisation of *G. pectinatus* in particular and other food resources has been shown to depend on the abundance of the resource. The rate at which *Neomysis mercedis* ingests both Copepoda and Cladocera is dependent on the abundance of the prey item (Edmondson and Murtaugh, 1980; Siegfried and Kopache, 1980), as well as the species of the prey (Edmondson and Murtaugh, 1980). The proportions of other prey types captured were probably related to the population densities and sizes of each prey type, and the electivity of the mysid for a prey species. The decreased contribution of benthic animals to the diet between November and February suggests that a seasonal change in the behaviour of the mysid may have occurred, as observed by Lasenby (1979).

Seasonal changes in the abundance of filamentous algae and *G. pectinatus* were observed and influenced ingestion. Kost and Knight (1975) showed both season and site specificity in ingestion by *Neomysis mercedis* to be dependent on the species consumed; this was presumably dependent on the influence of the environment examined on food availability. This observation offers a partial explanation of changes in the volumes of some different food types ingested; the site-specific differences in the total volumes of food ingested and the seasonal differences in ingestion may be subject to environmental influence (Le Magnen, 1967; Menge, 1972; Porter, 1977), affecting food availability and therefore the nature of the diet (Houston, 1973; Levinton, 1972; Rybock, 1978). However, many organisms do not show marked seasonality in diet (Odum and Heald, 1972). *Tenagomysis chiltoni* exhibited marked seasonal variation in the ingestion of filamentous algae, *Gladioferens pectinatus* and benthic prey items, but surprisingly, little variation in other food components.

While at any point in time, site-specific differences in ingestion by *T. chiltoni* may have been marked, over the whole study period within the region studied, some consistent trends were found in the observed diet. However, as the benthic fauna of Lake Ellesmere is more sparse in open water regions of the lake (Stout, 1969), and less saline habitats may contain a greater diversity of potential food organisms, variation between different regions may be more marked elsewhere in the lake. This aspect should be investigated when more information on the distribution of benthic organisms in Lake Ellesmere becomes available.

CHAPTER 7

GENERAL DISCUSSION

The main components of the diet of *Tenagomysis chiltoni* in Lake Ellesmere over the study period, in order of decreasing proportion of the total volume ingested, have been shown to be macrophyte detritus (47%), filamentous algae (27%), diatoms (12%), copepods (7%), insects (6%), amphipods (1%), and ostracods (0.1%). While the proportion contributed by each dietary component is known for few other species of the Mysidacea, several authors have commented on the identity of food fragments found in the digestive tracts of mysids (e.g., Mauchline, 1967-1971). These observations have been summarised by Mauchline (1980), whose table has been modified and is presented as Table 11.

Detritus, copepods and crustaceans generally are ingested by most of the mysid species investigated (Table 11). Algae in general, diatoms and terrigenous material also formed part of the diet of slightly fewer mysids. *T. chiltoni* therefore ingests similar dietary components to most other mysids investigated, with the notable additions of amphipods and insects. The ingestion of amphipods was thought to be restricted to mysid species having an adult length of between 10 and 77 mm, although several authors record unidentified crustacean fragments (Mauchline, 1980; Mauchline and Murano, 1977); however, the minimum adult length recorded for *T. chiltoni* is 8.5 mm (this study), and the smallest mysid which ingested the amphipod *Paracorophium lucasi* was 5.0 mm long. *T. chiltoni* is therefore the smallest of five species known to ingest amphipods. Only three species of mysids are known to ingest insects (Mauchline, 1980; this study), reflecting the usual unavailability of insects to this principally marine order. Only one other species is known to ingest ostracods (Mauchline, 1980).

The diet of the mysid *Neomysis mercedis* was originally estimated to consist principally of diatoms and detritus (Kost and Knight, 1975). But *N. mercedis* was subsequently re-examined by Siegfried and Kopache (1980), who concluded that carnivory accounted for over 90% of the food ingested by members of this species over 6 mm long and that herbivorous feeding may be important to the smaller mysids present. Both studies show diet changes with growth. Herbivory may be important to larger mysids of different

Table 11. Diets within the Order Mysidacea (after Mauchline, 1980). X = data from Mauchline (1980), 0 = this study, NR = not recorded in Lake Ellesmere.

Species	Detritus	Algae	Diatoms	Dinoflagellates	Tintinnids	Rotifers	Sponges	Polychaetes	Molluscs	Ostracods	Cladocera	Copepods	Amphipods	Crustacea	Carrion	Terrigenous Material	Insects	Faecal pellets	References
Acanthomysis sculpta		X										X		X					1
Antarctomysis maxima	X		X									X	X						1
Boreomysis sp.		X	X											X					1
Erythrops elegans	X		X	X															1
Erythrops serrata	X													X		X		X	1
Gastrosaccus psammodytes	X	X												X					1
Gastrosaccus spinifer	X											X	X						1
Leptomysis gracilis	X															X			1
Mesopodopsis slabberi	X													X					1
Mysidopsis almyra	X		X									X				X			2
Mysidopsis didelphys												X							1
Mysidopsis gibbosa				X								X							1
Mysis mixta	X		X									X	X						1
Mysis relicta	X	X	X								X	X		X			X		1, 3, 4
Neomysis integer	X	X	X			X						X	X	X	X	X	X		1
Neomysis intermedia	X	X	X			X					X	X		X		X			1
Neomysis mercedis		X	X	X	X	X	X				X					X			1, 5, 6
Paramysis arenosa	X		X	X										X		X			1
Praunus flexuosus	X	X	X					X				X		X					1
Praunus neglectus	X	X										X		X		X			1
Praunus spp.	X	X							X	X		X		X					1
Schistomysis kervillei	X			X								X		X					1
Schistomysis ornata	X			X										X		X			1
Schistomysis spiritus	X		X	X								X				X			1
Simiella pasifica	X										X	X		X					1
Spelaeomysis longipes	X	X	X											X					1
Taphromysis bowmani	X		X									X				X			2
Tenagomysis chiltoni		0	0	NR	NR	NR	NR				NR	0	0	0	0	0	0	0	

1 Mauchline, 1980.
2 Odum and Heald, 1972
3 Bowers and Grossnickle, 1978
4 Threlkeld *et al.*, 1980
5 Siegfried and Kopache, 1980
6 Edmondson and Murtaugh, 1980

species during phytoplankton blooms (Bowers and Grossnickle, 1978), or in the presence of abundant resources of ingestible live plants (this study). *Tenagomysis chiltoni* did not ingest large quantities of animal tissue. The study by Kost and Knight (1975) recorded only 739 crustacean fragments and 1249 animal fragments in 1500 complete intestinal tracts of the same species and in the same ecological system to the study by Siegfried and Kopache (1980) mentioned above, which suggests that the quantity of animal tissue consumed may vary considerably between different years, probably as a result of prey availability. It is therefore more important to understand why a food material is ingested rather than what is ingested. The supply of all food resources in the available habitats may determine feeding behaviour, as the increase in benthic feeding of *T. chiltoni* during winter suggests in this species. In *Mysis relicta* an association between resource abundance and its utilisation has been more clearly demonstrated (Edmondson and Murtaugh, 1980; Threlkeld *et al.*, 1980); this association may be remarkably precise (Correlation Coefficient = 0.89, Rybock, 1978). Thus, the availability of foods within the habitats available to a mysid has been clearly demonstrated to influence the ingestion of food by the mysid. Dietary composition is therefore not a constant but a dynamic variable dependent, for example, on the size of a consumer and the nature of the food supply. It is influenced by the life histories of the food resources (Glasser, 1978), as well as by the mysid's life history (this study) both in terms of the population structure existing at any time (which will influence the intensity and, to a degree, character of the resource utilisation) and in terms of the population density (which will affect the intensity of the resource utilisation). Unfortunately, it is not possible at present to assess the environmental impact of such changes as no information is available on the gut passage rates of *T. chiltoni*. This information is necessary to calculate consumption rates from the standing stocks of different food resources (Windell, 1978).

As samples were collected only during daylight hours (due to practical limitations), no information is available on the influence of daylight on the nature of the foods ingested. This influence may affect some species (e.g., *Mysis relicta*, Lasenby and Langford, 1973) but not others (Mauchline, 1980). The vertical migration of mysids into the upper levels of the water column at night is considered to be a feeding response (Bowers and Grossnickle, 1978). As Lake Ellesmere is shallow and turbulent, the water column is normally well mixed, which suggests that *Tenagomysis chiltoni* would derive little benefit from diurnal migration. *T. chiltoni*

may, however, migrate as an innate response to variations in the ambient light intensity. Thus, the influence of time of collection upon the observed diet is unknown.

The diet of *T. chiltoni* was determined by methods dependent on the preservation of, and identification of, characteristic fragments of foods ingested (Moore, 1977). With several types of food these fragments may be lost, too small for detection by the methods used, or damaged beyond recognition by the mastication of a mysid or the general preparatory techniques. Several large chlorophytes and two nematode worms were observed in the stomach of *T. chiltoni* during the study, but were almost unrecognisable. As these groups were abundant in the food resources at times, it must be noted that the small size of most solitary chlorophytes, and the presence of the nematodes below the surface of the mud, suggests that it is improbable that these organisms constituted more than a minor component of diet. Most other potential food items without hard parts were normally present in only modest quantities and in habitats inaccessible to *T. chiltoni*, so that the contribution to the diet of the mysid of foods which lost their identity prior to analysis is, at most, small. However, the eggs of fish and invertebrates were readily consumed in aquaria and as these eggs, especially those of amphipods, were at times moderately abundant, they may have contributed to the diet of the mysid. Some ingestion of faecal material may also have occurred. But the diet observed is thought to be a good approximation of the food of *T. chiltoni* in Lake Ellesmere.

Some species of mysids have been found to consume corpses of their own species (Cannon and Manton, 1927; Clutter and Theilacker, 1971); these species are not necessarily cannibalistic (Tattersal and Tattersall, 1951), and some may consume post-larvae of the same species (Clutter, 1969; Parker and West, 1979). Injured mysids may also be attacked and consumed (Green, 1970, cited in Kost and Knight, 1975). *T. chiltoni* was observed eating corpses of its own species in aquaria in conditions similar to those in the lake. A single endopod of *T. chiltoni* was found in the stomach contents of a mysid from the lake; this phenomenon is not, therefore, frequent in the feeding of *T. chiltoni*.

Coprophagy has been observed in *T. chiltoni* as in some other mysids (Mauchline, 1968; Parker and West, 1979). Levinton (1972) argued that faecal pellets, and the attendant microbial communities which colonise them (Hargrave, 1972), may form an important food source. Solution and bacterial

activity may reduce the amount of organic matter present in the faecal material (Johannes and Satomi, 1966), but the increased microflora present (Hargrave, 1976) may enhance the food value of a particle (Fenchel, 1970, 1972). This may explain the rejection of fresh faecal material observed in *T. chiltoni*. Faecal material was frequently present in water column and benthic food resource samples, and may have contributed small to moderate amounts of food to the mysids' diet.

Some more exotic components of the diet were also observed. The isopod *Austridotea benhami* (which was rarely ingested), insect larvae (other than chironomids) and some unusual types of algae were consumed. Such foods only contributed a miniscule proportion of the diet.

The consumption of lake detritus accelerates nutrient regeneration (Levinton, 1972; Saunders, 1977). The more rapid resorption of nutrients may contribute to the stability of a system (Fenchel, 1972). In a highly eutrophic lake such as Lake Ellesmere the consumption of macrophyte detritus, and the associated rapid return of the nutrients which it contains to the system, probably only marginally increases the productivity of an already highly productive system, and would not greatly affect the stability of the lake. However, it is interesting to note that both the abundant supply of allochthonous detritus within lake and dissolved nutrients in the run-off from the catchment area may contribute to the eutrophication of the system. As *T. chiltoni* probably consumes only a fraction of the detritus present, this species is possibly not of great significance to nutrient cycles within the lake.

The feeding success of an individual is not only of interest in the short term. The nutritional history of the parent may exert a marked influence on the number of offspring produced (e.g., Holling, 1969). Because the food obtained by an individual at any time may limit its growth (Lasker, 1966) and brood size is highly dependent on female length in many species of mysids (Mauchline, 1980), including *T. chiltoni*, it follows that fecundity may depend on nutritional history in the Order Mysidacea. As the composition of the food resource is affected by the life-histories of its components (Glasser, 1978), so are the intensity and character of predation influenced by a predator's life-history. Seasonal fluctuations in the numerical density and, to a lesser extent, the length-frequency structure of *T. chiltoni* populations observed in Lake Ellesmere will produce changes in the intensity and character of both its predation and its ecological impact on its other possible food sources.

Ingestion by *T. chiltoni* was, however, not solely dependent on the population of mysids present at any given point in time, but in many cases was shown to be highly dependent on the availability of foods, especially within the water column. Food selectivity was also influenced by the physical nature of a food particle, as has been found in other mysids (Edmondson and Murtaugh, 1980, *Neomysis mercedis*; Bowers and Grossnickle, 1978, *Mysis relicta*), and in many other studies of invertebrates (e.g., Nival and Nival, 1976; Parsons *et al.*, 1967). The availability of food was not however the single environmental determinant of diet; diet may also be strongly influenced by wave action and other environmental parameters (e.g., temperature, Windell and Bowen, 1978). In particular, salinity is thought to influence the population structure, population density and foods ingested by *Tenagomysis chiltoni*.

Dietary selection of other animal groups may be a complex interaction of individual and environmental parameters (Berg, 1979; Carefoot, 1973; Dethier, 1970; Estabrook and Dunham, 1976; Frost, 1977; Harper, 1967, etc.), which must be comprehensively investigated in order to understand why certain foods were ingested. While no evidence of food preference or choice was found in this study, an interaction of mysid size, operating partly through sexual length differences, and population density is suggested. Seasonal successions in the population have been shown to influence the diet of *T. chiltoni*, and may exert an influence on the availability of different foods when the density of the mysid population is high. Environmental variables such as wave action, salinity, and presumably temperature, affected the availability and consumption of foods. The availability, nature and abundance of different foods varied markedly between the sites studied, and influenced the observed diet of *T. chiltoni*. All these, and possibly other factors (such as diurnal rhythms), may interact to produce the observed diet of *T. chiltoni* in Lake Ellesmere. It is therefore apparent that if we know merely what foods were ingested at a given locality at specified times, the results and conclusions cannot be extrapolated to predict what is likely to occur in another locality, or even the same locality at another time.

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POSTSCRIPT

The life of plants is one continuous solitary meal,
and ruminants
hardly interrupt theirs to sleep or to mate, but most
predators feel
ravenous most of the time and competitive
always, bolting such morsels as they can contrive
to snatch from the more terrified: pack-hunters do
dine *en famille*, it is true,
with protocol and placement, but none of them play host
to a stranger whom they help first. Only man,
supererogatory beast,
Dame Kind's thoroughbred lunatic, can
do the honors of a feast.

W.H. Auden (June 1964)
in Collected Poems
Edited by Edward Mendelson,
Faber and Faber (London) 1976.

"The thing that the ecologically illiterate don't realise about an ecosystem ... is that it is a system. A system! A system maintains a certain fluid stability that can be destroyed by a mis-step in just one niche. A system has order, a flowing from point to point. If something dams that flow, order collapses.... That's why the highest function of ecology is the understanding of consequences."

Pardot Kynes, First Planetologist
of Arrakis in "Dune" by Frank
Herbert (1965). New English
Library, London.